

THE DISJUNCT BRYOPHYTE ELEMENT
OF THE GULF OF ST. LAWRENCE
REGION: GLACIAL AND POSTGLACIAL
DISPERSAL AND MIGRATIONAL HISTORIES

CENTRE FOR NEWFOUNDLAND STUDIES

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**The Disjunct Bryophyte Element of the
Gulf of St. Lawrence Region:
Glacial and Postglacial
Dispersal and Migrational Histories**

By

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Abstract

The Gulf St. Lawrence region has a bryophyte flora of 698 species. Of these 267 (38%) are disjunct to this region from western North America, eastern Asia, or Europe. The Gulf of St. Lawrence and eastern North American distributions of the disjuncts were analysed and their possible migrational and dispersal histories during and after the Last Glaciation (Wisconsin) examined. Based on eastern North American distribution patterns, the disjuncts fell into 22 sub-elements supporting five migrational/dispersal histories or combinations of these : (1) migration from the south, (2) migration from the north, (3) migration from the west, (4) survival in refugia, and (5) introduction by man.

The largest groups of disjuncts had eastern North American distributions supporting either survival of bryophytes in Wisconsin ice-free areas of the Gulf of St. Lawrence or postglacial migration to the Gulf from the south. About 26% of the disjuncts have complex histories and their distributions support two histories. These may have migrated to the Gulf from the west and/or north, or from the west and/or survived glaciation in Gulf ice-free areas. The eastern North American distributions of some species in these groups suggests that survival in ice-free areas best explains their presence in the Gulf of St. Lawrence. Anthropogenic introduction to the Gulf and migration from the north are

relatively unimportant migrational/dispersal histories for disjuncts in the region. No bryophyte sub-elements supported the hypothesis of long distance dispersal to the Gulf of St. Lawrence.

Within the Gulf of St. Lawrence, species having migrated from the south generally show widespread distributions or occur primarily in the southern portions of the study area. Bryophytes introduced to the Gulf by man occur in eastern Newfoundland and in central Nova Scotia. The bryophytes in the remaining groups show generally similar patterns; they are restricted to the northern half of the study area, or show small disjunctions between western Newfoundland, Gaspé and, occasionally, Cape Breton.

Important habitats for disjunct bryophytes are late snowbeds and limestone barrens. The disjunct bryophytes in late snowbeds are primarily montane species, whereas the disjunct bryophytes in the limestone barren habitat are predominantly of arctic affinity. The disjunct bryophytes in the snowbed habitat provide some of the strongest evidence for survival of bryophytes in Gulf ice-free areas.

The importance of disjunctions to the phytogeography of the Gulf of St. Lawrence varies with geographic scale. Continental disjunctions are best explained as resulting from climatic and geological changes occurring since the Tertiary whereas disjunctions at the eastern North American scale provide the

best evidence for solving problems relating to Wisconsin bryophyte dispersal and migrational histories in the Gulf. Bryophyte disjunctions within the Gulf are explained adequately by climatic and ecological factors operating during the Holocene.

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Chapter 1

INTRODUCTION

1.1. Purpose

A disjunct species distribution is one in which two or more populations are more widely separated than the normal dispersal capability of that species would allow (Cain 1944). Such distributions are particularly important to historical biogeography (Dansereau 1957). In Europe and North America plant disjunctions have been used to indicate Tertiary relics (Li 1952; Sharp 1972a, 1972b) and survival in glacial refugia (Gjaerevoll 1963; Steere 1965; Brassard 1971).

Bryophytes, comprising the mosses (Class Bryopsida) and hepatics (Class Hepaticopsida), have been considered better phytogeographic indicators than vascular plants because their small size and restriction to microhabitats may allow them to persist in an area long after the general climate has changed, and also because of their presumed slower evolutionary rates (Schuster 1958a; Anderson 1963; Steere 1965; Crum 1966, 1972).

The Gulf of St. Lawrence region of eastern Canada has approximately 700 species of bryophytes; about 40% of these have distributions showing major disjunctions between or within the Northern Hemisphere continents. Many of

these bryophytes also show disjunctions to a greater or lesser extent in the eastern North American portion of their range, and even within the Gulf of St. Lawrence region itself. This large disjunct element has not been investigated previously in relation to dispersal and migratory history theories in the Gulf of St. Lawrence region during and after the Last Glaciation.

The purposes of this study were:

1. To analyse the present-day distributions of these disjunct bryophytes for the Gulf of St. Lawrence and eastern North America, and
2. To examine possible dispersal and migrational histories for the disjunct bryophyte element during and after the Last Glaciation.

The term "Last Glaciation" will be used throughout this study because of the difficulties in recognizing which of several Wisconsin glacial events was most important in the disruption of species ranges. It is generally recognized that, in general usage, "Last Glaciation" refers to the Late Wisconsin (ca. 30-10 ka B.P.), although it may also refer to earlier Wisconsin glaciations, or to the whole Wisconsin (ca. 80-10 ka B.P.).

1.2. Description of the Study Area

Physiography and Geology. The study area (Figure 1-1) includes the following land regions in the Gulf of St. Lawrence: the three Maritime Provinces of Canada (Nova Scotia, New Brunswick, Prince Edward Island), Gaspé Peninsula east of the Matapedia River, the Quebec North Shore, southern Labrador along the Strait of Belle Isle (north to 52°N), Newfoundland, Anticosti Island, the Magdalen Islands, St. Pierre and Miquelon, and Sable Island. The total land area is approximately 317,000 km².

The following description of the geology and physiography of the study area is derived mainly from Bird (1972) and Bostock (1970).

Three physiographic regions are represented in the study area: the Appalachian Region, the Canadian Shield, and the St. Lawrence Lowlands (Figure 1-2).

The Appalachian Region comprises the largest portion of the study area, and is dominated by peneplain or plateau surfaces which are inclined southeastward. Several highland, upland and lowland regions are present (Bird 1972; Bostock 1970). The highlands vary in elevation from 200 metres to greater than 1000 metres and the highest point reached is at Mont Jacques-Cartier (1268 m) in Gaspé. The highlands and uplands may be either rolling peneplain surfaces such as in the Shickshock and Long Range Mountains, or rugged, rocky terrain as is characteristic for much of Newfoundland.

Figure 1-1. Map of the Gulf of St. Lawrence study area showing the major regions referred to in the text.

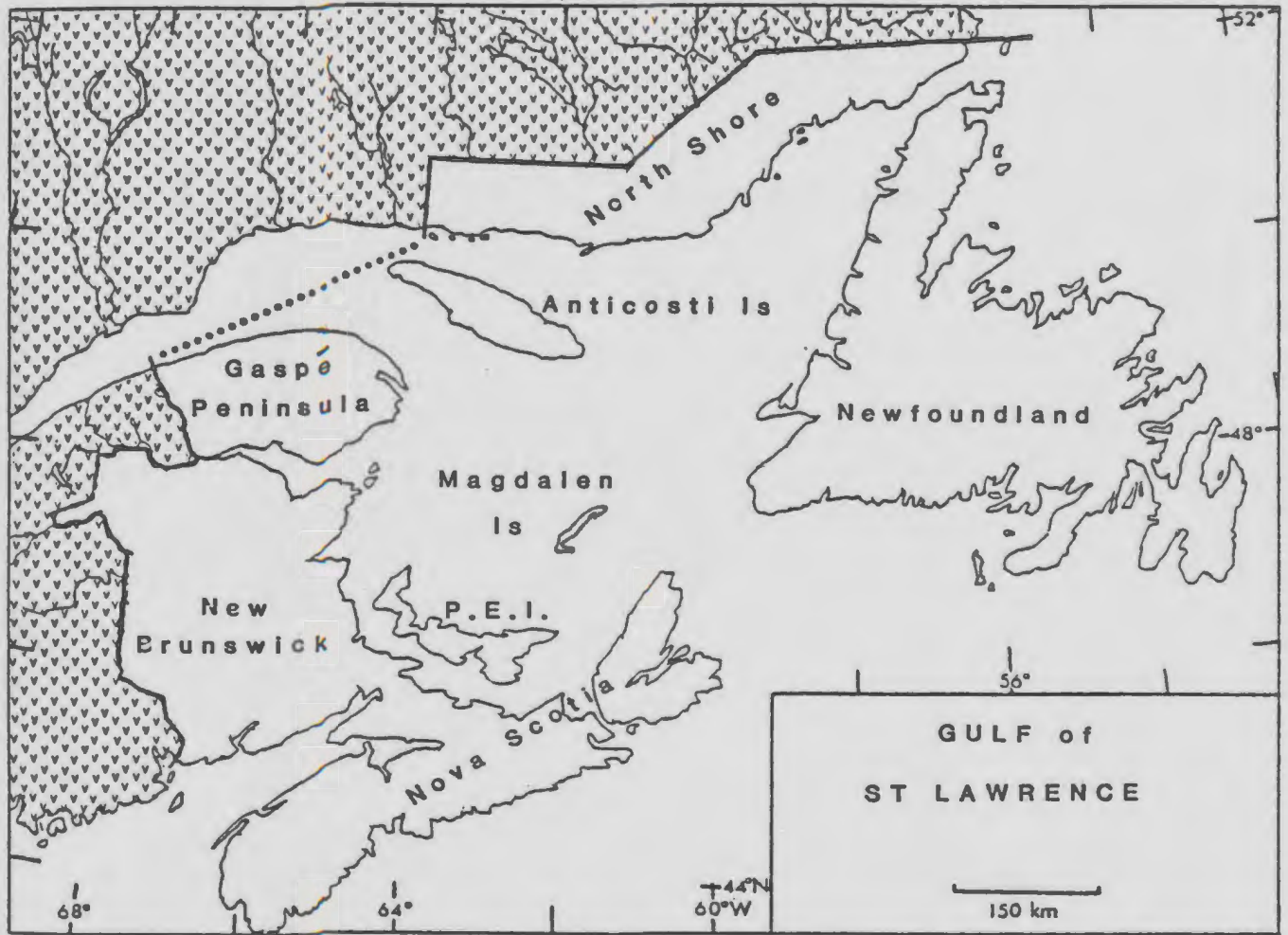
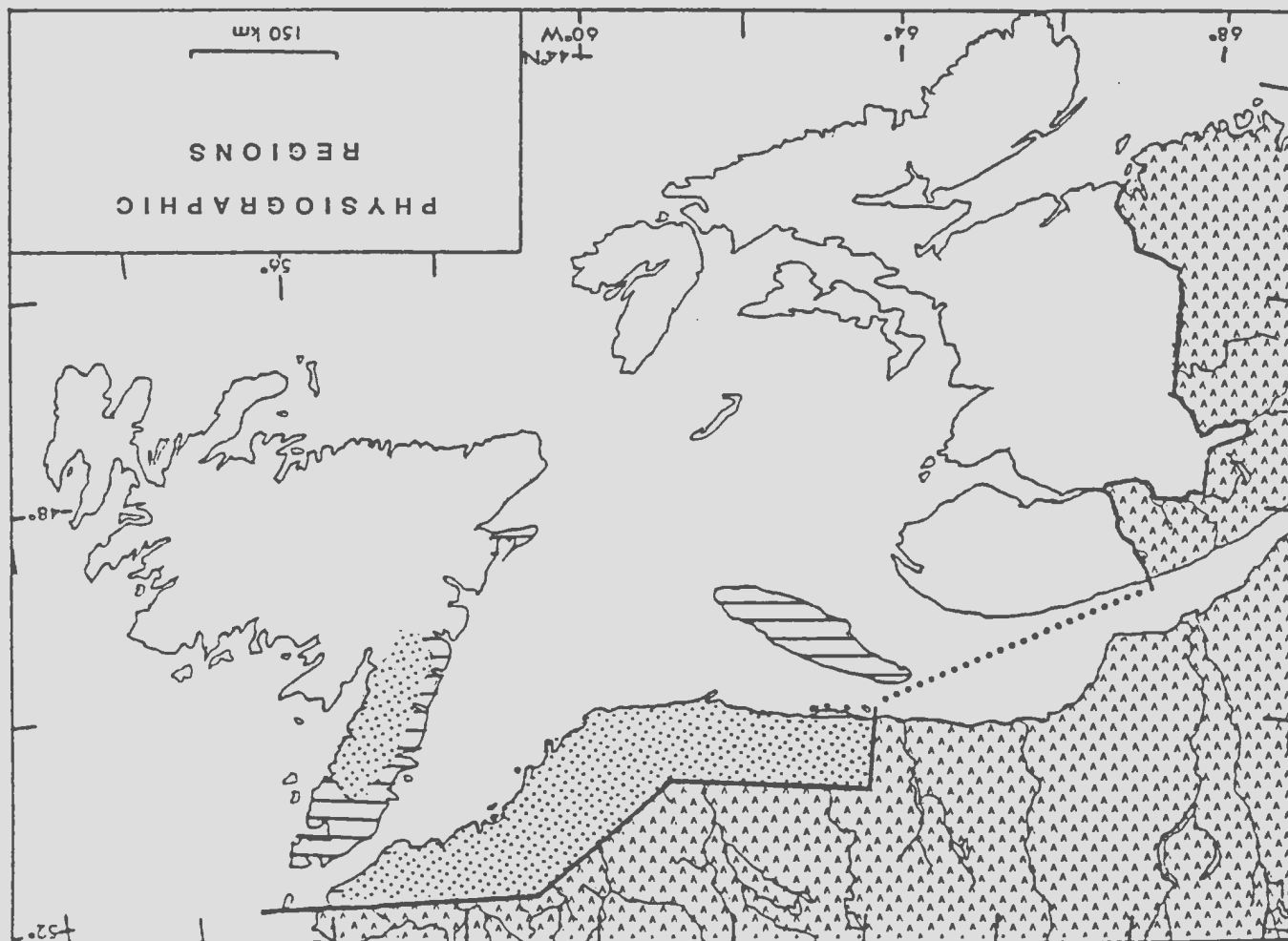


Figure 1-2. The physiographical regions of the Gulf of St. Lawrence.

Horizontal lines denote the St. Lawrence Lowland; stippling the Canadian Shield; blank is the Appalachian region.



The lowland areas of the Appalachian Region are represented by the Maritime Plain stretching along the northern coasts of New Brunswick and Nova Scotia, and includes Prince Edward Island and the Magdalen Islands and Newfoundland's Central Lowlands. These are characterized by a gently undulating topography with relief seldom greater than 200 metres.

The Appalachian Region includes sedimentary, igneous, and metamorphic rocks whose lithologies range from acidic to ultramafic. The geology of the region is complex. Acidic rocks, including granites, some gneisses, shales, sandstones, and quartzites, underlie the major portion of the region. Major areas of igneous or metamorphic basic rocks, mainly gabbros and amphibolites, are present in the highlands of western Newfoundland and in central Gaspé where they are associated with ultramafic masses. Basic rocks also underlie portions of central Newfoundland, Cape Breton Island and northern New Brunswick. Major exposures of calcareous rock are also found along the coast of Gaspé Peninsula and western Newfoundland. Ultramafic rocks, primarily pyroxenite, dunite, and serpentinite, form the masses of several serpentine mountains in Gaspé and western Newfoundland. Several smaller ultramafic rock exposures are also found on the Baie Verte Peninsula of Newfoundland and in central Newfoundland.

The North Shore of the St. Lawrence, with the exception of the areas near the Mingan Islands and the northwestern shore of the Strait of Belle Isle, is part

of the Laurentian Region of the Canadian Shield (Bostock 1970). Inliers of Canadian Shield rocks are also found in northwestern Newfoundland where they form the backbone of the Long Range Mountains. In the Gulf region, the shield areas are undulating peneplains dissected by river valleys. In most areas, the shield rises abruptly from near sea level to elevations greater than 600 metres along fault scarps. In western Newfoundland, the Long Range Mountains are breached by spectacular fiord-like valleys whose walls rise in places to almost 600 metres above the valley floors. Precambrian rock, mainly granitic gneiss, underlie most of this physiographic region.

The St. Lawrence Lowlands include Anticosti and the Mingan Islands, the Newfoundland Coastal Lowland (extending along the western shore of the Northern Peninsula), and the Port-au-Port Peninsula, plus several smaller areas bordering the Gulf and the Strait of Belle Isle. Relief is generally low, with elevations less than 160 metres; however, at Port-au-Port and in the St. John Highlands (western Newfoundland) relief exceeds 600 metres. The rocks in this physiographic region are mainly Paleozoic carbonates.

Glacial History. Much of the literature on the glacial history of the Gulf of St. Lawrence has focused on the extent of the Wisconsin Glaciation, and in particular on the geomorphological evidence for unglaciated areas in the region (Ives 1978, Grant 1977a). Geomorphological evidence for such unglaciated areas

is based mainly on the presence of blockfields of highly weathered bedrock (felsenmeer) on some highland summits, particularly in Gaspé and western Newfoundland. The time required for the development of these blockfields has been at the centre of the controversy.

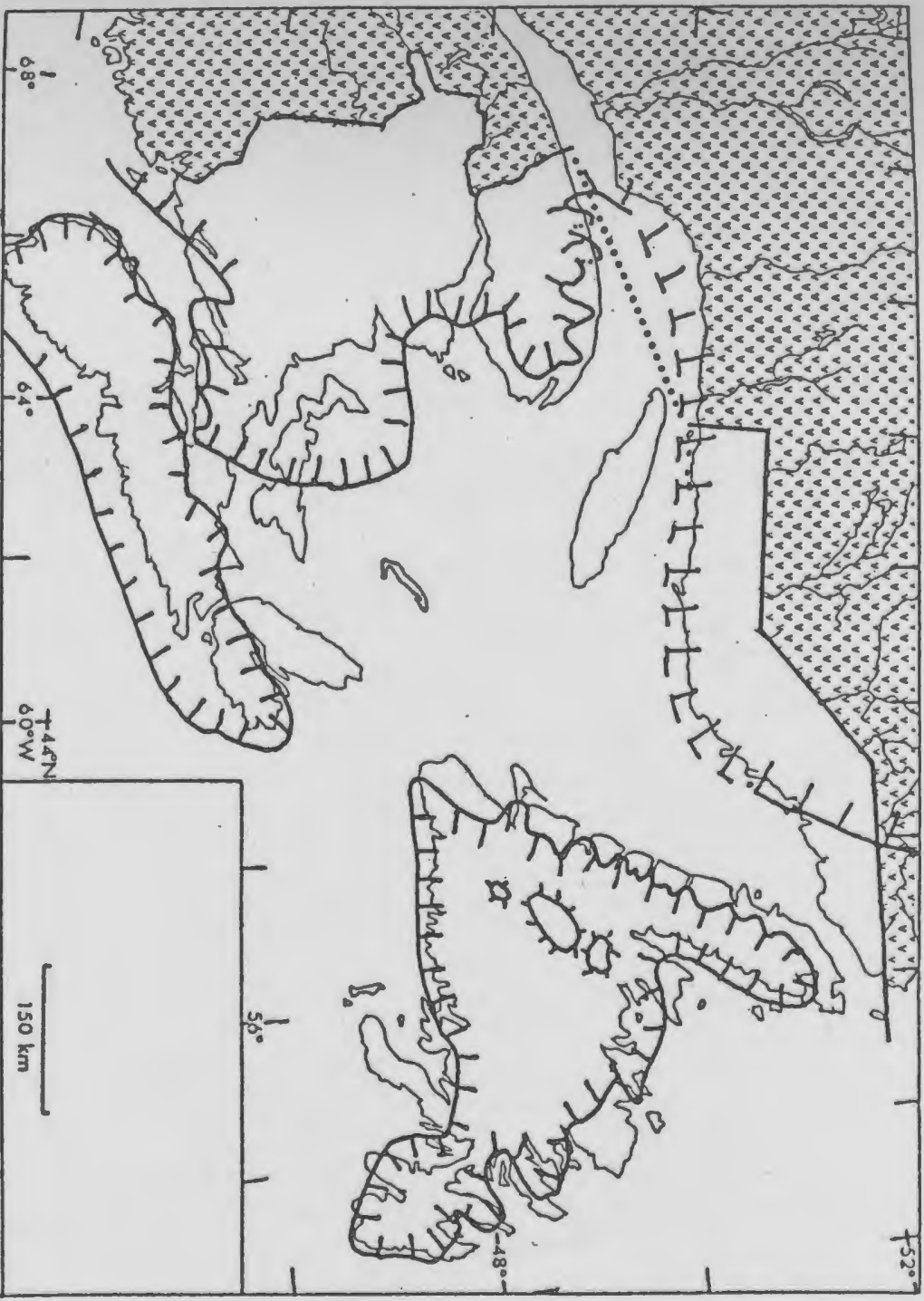
Coleman (1922, 1926) was the first to describe felsenmeer in the region and believed such rock debris would have been aerially exposed since the previous glaciation to account for its highly weathered aspect. Later workers (MacClintock and Twenhofel 1940; Flint *et al.* 1942; Alcock 1944), rejected Coleman's appraisal. Flint *et al.* (1942), for instance, believed the felsenmeer was much younger, and that the blockfields on Tabletop Mountain in Gaspé "...presumably originated in postglacial time". In Gaspé and western Newfoundland, the presence of relatively 'fresh' erratics and glacial striae supported MacClintock and Twenhofel's (1940) concept of complete glacial overriding.

The controversies for or against a complete ice cover in the Gulf are continuing. Recent studies based on more extensive data have supported Coleman's original ideas. In western Newfoundland, for instance, three altitudinal weathering zones are recognized (Brookes 1977; Grant 1977a). The uppermost zone is a felsenmeer zone thought to have escaped the effects of glacial ice since the last interglacial (ca. 120,000 yrs. B.P.) and the middle zone, also highly weathered, since probably the mid-Wisconsin (Grant 1977a). Only the lowermost

zone shows signs of recent glacierization and was probably covered during the Late Wisconsin. In addition to the weathering zones, dated marine features and low level moraines point to a minimal ice cover during the Late Wisconsin. Probable ice-free areas include many parts of Newfoundland (Brookes 1977; Grant 1977b; Tucker and McCann 1980; Leckie and McCann 1983), Cape Breton Island (Grant 1977b), Gaspé (Lafrenière and Gray 1981), as well as the North Shore and southern Labrador (Fulton and Hodgson 1979) (Figure 1-3). In contrast, Mayewski *et al.* (1981) have stressed the concept of a complete ice cover over the Gulf during the late Wisconsin using as principal argument that some of the dated marine deposits used by Brookes (1977) and Grant (1977b) do not represent the maximum ice limits during that time.

Climate. Two climatic regions are represented in the study area, Atlantic and Boreal (Hare and Thomas 1979). The Atlantic region includes the Maritime Provinces and insular Newfoundland. Prevailing circulation is westerly, resulting in a wider fluctuation of daily and seasonal temperatures than expected in typically maritime climates. Thus, this region has a continental climate, despite the abundant precipitation, (1100 to 1500 mm yearly). Mean annual temperatures range from 0°C to 8°C (Canada, Dept. of Transport, Meteorological Branch 1969). The sea modifies the local temperature, particularly along the eastern coasts of Newfoundland and Nova Scotia, where temperatures are lowered by the cold waters of the Labrador current.

Figure 1-3. Late Wisconsin ice limits in the Gulf of St. Lawrence
(redrawn from Grant (1977a) and Rogerson (1981)).



The Gaspé Peninsula, Anticosti, and the North Shore are within the Boreal climatic region of Hare and Thomas (1979) with cold winters and a mean annual temperature of below 0°C. Precipitation is generally low during all seasons, from 900 to 1000 mm annually (Canada, Dept. of Transport, Meteorological Branch 1969).

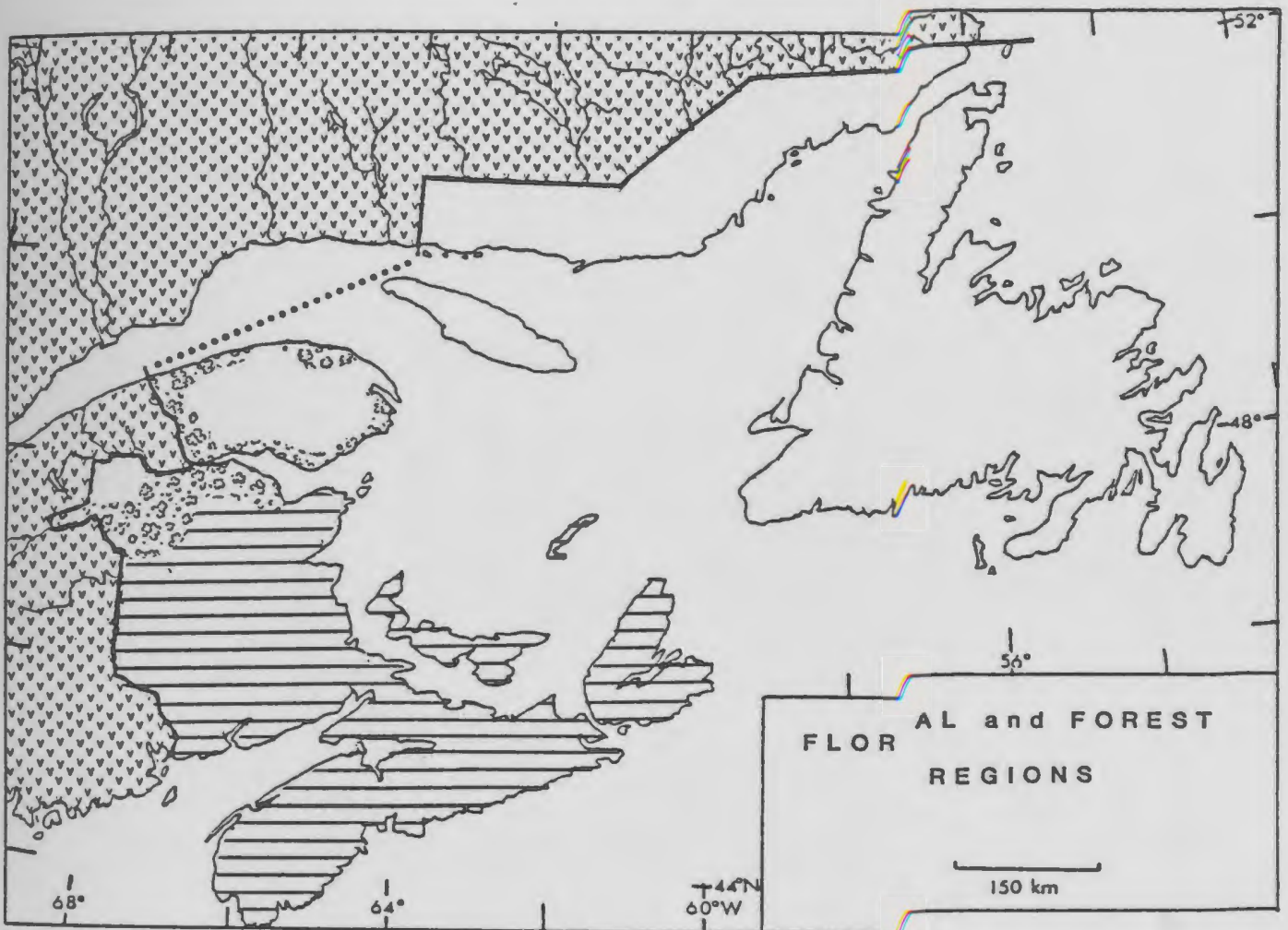
Detailed climatic data for Atlantic Canada have recently been published by Environment Canada, Atmospheric Environment Service (1982) and local treatments can be found for Newfoundland and Labrador in Banfield (1981, 1983) and for Gaspé in Wilson (1971).

Vegetation and Vascular Flora. The study area includes three forest regions (Rowe 1977): Boreal, Great Lakes-St. Lawrence, and Acadian (Figure 1-4). These correspond exactly with the floristic regions of Scoggan (1978).

The boreal forest region is characterized by the dominance of conifers, principally *Picea mariana* (Mill.) B.S.P., *P. glauca* (Moench) Voss., and *Abies balsamea* (L.) Mill. Deciduous trees such as *Betula papyrifera* Marsh., *Populus tremuloides* Michx. and *P. balsamifera* L. are generally admixed. Forest-tundra vegetation is found along both sides of the Strait of Belle Isle, including the tip of the Northern Peninsula of Newfoundland, and consists of tundra barrens intermingled with stunted forests comprised primarily of *Picea glauca* and *P. mariana*.

Figure 1-4. The floral and forest regions of the Gulf of St. Lawrence.

Horizontal lines indicate the Acadian Forest; mottling is the Great Lakes-St. Lawrence Forest Region; blank is Boreal Forest.



Picea rubens Sarg. is the characteristic tree of the Acadian forest region. Frequently associated with it are *Abies balsamea* and *Betula alleghaniensis* Britton, while *Acer saccharum* Marsh., *Pinus resinosa* Ait., *P. strobus* L., *Tsuga canadensis* (L.) Carr., and *Fagus grandifolia* Ehrh. are occasional components. Hardwood trees are more abundant than in the boreal forest, and may form communities covering extensive areas, such as in eastern New Brunswick and central Nova Scotia.

The St. Lawrence-Great Lakes forest region occupies the smallest area in the Gulf, being restricted to coastal and eastern Gaspé Peninsula and northern New Brunswick (Figure 1-4). *Pinus resinosa* and *P. strobus* are characteristic of this forest region, as well as *Tsuga canadensis* and *Betula alleghaniensis*. Associated with them are *Acer saccharum*, *A. rubrum* L., *Quercus rubra* L., *Tilia americana* L. and *Ulmus americana* L.

In all three forest regions, the continuous forest cover may give way to heath barrens or peatlands. Heath barrens are dominated by ericaceous shrubs such as *Empetrum nigrum* L., *Gaylussaccia baccata* (Wang.) K.Koch., and *Kalmia angustifolia* L., and often characterized by the occurrence of arctic-alpine species such as *Diapensia lapponica* L., *Loiseleuria procumbens* (L.) Desv., and *Rhododendron lapponicum* (L.) Wahlenb. Heathland vegetation occurs in Gaspé and the Maritimes, but is especially important in Newfoundland where it

covers 20% of the island (Meades 1983). In all areas around the Gulf, heath vegetation is found mainly along the exposed coasts or at higher elevations. The ecology of Newfoundland heath barrens are reviewed by Meades (1983), and Strang (1972) discussed their ecology in Nova Scotia.

Both major types of peatland (bogs and fens) are present in the study area, although bogs are more frequent. The peatlands of Canada have been provisionally mapped (Wetland Working Group 1981). The common bog type in the study area is the raised domed bog which occurs in most regions. In southern Newfoundland, however, slope and basin bogs predominate. A detailed review of the classification of peatland types in Newfoundland is found in Wells and Pollett (1983), but relatively little work has been done on the peatlands elsewhere in the Gulf region (D. Wells, personal communication, 1983).

The first postglacial records of tree genera in the Maritimes are of *Populus* and *Betula* at about 12,600 yrs. B.P. (Mott 1975), although *Picea* and *Abies* dominated by 11,500 yrs. B.P. (Holland 1981). In northern Gaspé, arboreal invasion began ca. 10,700 yrs. B.P., first by *Populus*, followed by *Picea* and *Abies* (Labelle and Richard 1981). The arrival of *Picea* to Newfoundland (Avalon Peninsula) is considerably later, about 8,300 yrs B.P. (MacPherson 1982). Delcourt and Delcourt (1981) and Delcourt *et al.* (1983) have summarized the postglacial expansion northwards of boreal and temperate forests.

There is no single list of the vascular plants of the Gulf of St. Lawrence region. Scoggan (1950) listed 1216 species from Gaspé Peninsula, and there are slightly less than 2000 species in Nova Scotia (Roland and Smith 1969), and about 1260 species in Newfoundland (Rouleau 1978).

Bryophyte Flora. The bryophyte flora of the Gulf of St. Lawrence is one of the better known in Canada. With the exception of the Quebec North Shore and Anticosti Island, bryologists have collected extensively in all portions of the study area. In addition, two recent moss floras (Crum and Anderson 1981; Ireland 1982) and a liverwort flora (Schuster 1966, 1969, 1974, 1980) include the region. There are no endemic bryophyte species yet known from the Gulf of St. Lawrence region as defined here (Figure 1-1).

Most of the early collections made in Gaspé, the Magdalen Islands, Anticosti, and the Mingan Islands, have been cited in the bryophyte catalogue of Lepage (1943, 1944, 1945, 1946). The major collections made in Gaspé since then by J. Kucyniak and F. Leblanc, as well as those of H. Crum and H. Williams (in 1960) remain largely unpublished, although Kucyniac (1952a, 1952b, 1952c, 1954, 1958, 1961) published several additions to the moss flora of Gaspé. More recently, floristic and ecological studies have resulted in publication of bryophyte lists for the Mingan Islands (Grondin and Melançon 1980), the Magdalen Islands (De Sloover 1976), and Bonaventure Island (Comeau 1966).

The first large collection of bryophytes made in Newfoundland was that of A.C. Waghorne during the latter part of the 19th century. In 1949, R. Tuomikoski made extensive collections around the island and this visit resulted in the first annotated lists for Newfoundland hepatics and mosses (Buch and Tuomikoski 1955; Tuomikoski *et al.* 1973). Since 1970, G.R. Brassard and his collaborators have made numerous additions to the Newfoundland bryophyte flora. Brassard (1983a, 1984a) has completed bryogeographic analyses of Newfoundland as well as a revised checklist of Newfoundland mosses (Brassard 1983b). Lists of the bryophytes of Labrador have also been compiled (Brassard and Williams 1975; Brassard and Weber 1978a).

Numerous persons have collected bryophytes in the Maritime Provinces or published on them (listed in Ireland 1982). The major collections include those of M.S. Brown, J. Erskine, J. Fowler, H. Habeeb, R.R. Ireland, J. Macoun, and W.B. Schofield. The earliest published report seems to be that of Sommers (1878), although the first major contribution was that of Macoun (1892, 1902). The first moss flora for the region was published by Erskine (1968) for Nova Scotia. Lists of mosses for each Maritime province county was recently published by Ireland (1982).

1.3. Review of Theories on the Migrational Histories of Disjunct Plants in the Gulf of St. Lawrence Region

Most of the explanations for the presence of a disjunct plant element in the Gulf of St. Lawrence region come from studies of vascular plants, and usually focus on the dispersal and migrational histories of these plants during and after the last (Wisconsin) glaciation.

Fernald (1911, 1925) was first to bring attention to the large disjunct plant element in the Gulf of St. Lawrence region. In his long and important studies of the region, he enumerated more than 300 vascular plants with isolated occurrences in the Gulf which were disjunctive to the North American Cordillera or to Europe. In addition, Fernald described many Gulf of St. Lawrence endemics whose taxonomically closest allies were found in the mountains of western North America. To explain the presence of the disjuncts and endemics in the Gulf, Fernald (1925) hypothesized that the plants had survived glaciation in ice-free enclaves (nunataks), persisting near where they survived, without extending their ranges postglacially. This hypothesis was later named the "nunatak hypothesis" (Wynne-Edwards 1937).

Wynne-Edwards (1937, 1939) strongly opposed Fernald's nunatak hypothesis stressing that certain ecological requirements of the rare plants explained their present-day patterns of distribution. He showed Fernald's disjuncts to be

restricted to soils derived from basic rocks, and, since these rocks were discontinuously distributed in North America, then plants restricted to them would necessarily also show discontinuous distributions. As an alternative to the nunatak hypothesis, Wynne-Edwards (1937) suggested that the rare disjunct element in the flora had survived the glaciation south of the icesheet, and migrated northward to the Gulf postglacially. Wynne-Edwards' (1937) opinions and observations were supported by many others (Griggs 1940; Scoggan 1950; Böcher 1951; Rune 1954; Damman 1965; Hounsell and Smith 1968; Drury 1969).

Marie-Victorin (1938) proposed two other hypotheses. In the "rainbow explanation", he suggested that the Cordilleran disjuncts are Arcto-Tertiary arctic-alpine plants that migrated south along both sides of the North American continent, became extinct in Arctic Canada and persist at the "ends of the rainbow". This explanation is similar to one stated by Wynne-Edwards (1937, p. 41). However, Marie-Victorin's theory emphasized the ancient origin of these plants whereas Wynne-Edwards' explanation accounted only for the present-day distribution.

Schofield (1969) also emphasized the possible ancient origin of the Cordilleran element and his explanation is that "...the eastern representatives are remnants of a more widespread flora of the past, possibly of pre-Pleistocene arctic-alpine distribution in North America".

In Marie-Victorin's (1938) "sidewalk explanation", some of the disjuncts are presumed to have migrated eastwards along the edge of the receding icesheet in a tundra corridor (sidewalk) extending from the Cordillera to the Gulf of St. Lawrence. This explanation received support from Raymond (1950), Rousseau (1953), and Whitehead (1972). Whitehead (1972) states that the disjuncts in the Gulf region may be thought of as "...the last remnants of this late-Pleistocene and early-postglacial eastward and then northward dispersal of Cordilleran species".

A similar hypothesis (Butters and Abbé 1953; Rousseau 1953; Soper and Maycock 1963; Miller 1980a, 1980b; Given and Soper 1981), applied mainly to Lake Superior disjuncts, has eastward migration playing a secondary role. The hypothesis proposes the arctic-alpine and Cordilleran plants to be relics from a more widespread tundra vegetation fronting the retreating icesheet. With ameliorating climate, the tundra vegetation gave way to forest communities and the arctic-alpine and Cordilleran plants became restricted to refuges where they are still found today.

The evidence given for the tundra sidewalk hypotheses is the present occurrence of intermediate stations in the Great Lakes for many Cordilleran vascular plants (Butters and Abbé 1953; Soper and Maycock 1963; Marquis and Voss 1981; Given and Soper 1981) and is supported by palynological evidence (Delcourt and Delcourt 1981; Delcourt *et al.* 1983).

Long range dispersal, either natural or by man, has been considered an explanation for some disjunctions. Of the two possibilities, the transport of plant species by man has received the most attention. Plant introductions of European or Eurasian species presently showing a disjunction across the North Atlantic Ocean were shown to be important in the floras of Nova Scotia (Roland 1947) and Newfoundland (Lindroth 1957). The plants introduced to Gaspé were treated by Rousseau (1968). Most of the plants were probably brought from Europe either in ship ballast, or inadvertently transported with agricultural products (Roland 1947; Lindroth 1957; Rousseau 1968; Roland and Smith 1969).

Natural long distance dispersal was discussed for disjuncts with Amphiatlantic distributions by Dahl (1963) and Löve (1963). Both workers rejected this hypothesis, showing that the dispersal mechanisms of Amphiatlantic plants would not account for their present distributions. Recently, however, Bouchard *et al.* (1977) have suggested that natural long distance dispersal might explain the occurrence of one rare disjunct fern in western Newfoundland, although they did not give any supportive evidence.

Changing taxonomic concepts and more extensive distributional data have substantially reduced the numbers of Gulf of St. Lawrence disjuncts or endemics listed by Fernald (1925). Both Drury (1969) and Rousseau (1974) re-analyzed Fernald's data and arrived at much reduced numbers of species supporting

Fernald's hypothesis. Drury (1969) pared Fernald's original list of some 406 species and 136 varieties of endemics and disjuncts to 40 or 50 species, while Rousseau (1974) further reduced the list to 14 species. Drury (1969) also questioned the relative importance of so few critical species.

Although the nunatak hypothesis as formulated by Fernald has been abandoned by most phytogeographers, there are still some who favour the concept of survival in refugia to account for the presence of disjuncts. Morisset (1971) in particular suggested that refugia on the adjacent continental shelf could explain the presence of many of the disjunct vascular plants in the Gulf of St. Lawrence.

The disjunct bryophytes of the Gulf have received little attention as compared to the vascular plants, and ideas concerning the origin of their distributions in North America have been presented only in very general terms.

Schofield (1969, 1980) has provided possible explanations for several of the disjunct groups occurring in the Gulf. Of the "Cordilleran disjuncts", he (Schofield 1969) suggests that they probably survived south of the icesheet, but possibly also in nunataks or coastal refuges, migrating northward to their present sites with the retreat of the icesheet.

Schofield (1969) explains circumalpine distributions similarly and adds the possibility of long range dispersal for this group. Long range dispersal is also

considered the most plausible explanation for Amphiatlantic moss distributions (Schofield 1980), although not all such distributions could be explained in this way.

Disjunct bryophytes with intermediate stations near the Great Lakes were first discussed by Steere (1937, 1938). The phytogeography of hepatics with such distributions were treated in detail by Schuster (1958a, 1958b, 1984), and the mosses by Crum (1966, 1972). While Schuster (1958a, 1958b, 1984) has emphasized the "Driftless Area" of western Wisconsin and southeastern Minnesota as a refugium from which the hepatics colonized suitable Great Lakes sites postglacially, Crum (1966, 1972) believed that the disjuncts are relics of tundra vegetation which bordered the icesheet during the glacial retreat. The study of sub-fossil bryophyte and vascular plant assemblages recovered in Wisconsin, New York and Vermont dated between ca. 11,000-12,500 yrs. B.P., have been interpreted as remnants of a widespread tundra environment fronting the icesheet during this late glacial period (Miller 1980a). Some of the species found as sub-fossils show present disjunctions between the Great Lakes and the Gulf.

Brassard (1984a) has recently discussed postglacial dispersal of mosses into Newfoundland from the north, through Labrador. He states that this may have been important for boreal and arctic species presently reaching their southern limits in Newfoundland.

Belland (1981), Belland and Brassard (1980a), Brassard and Hooper (1981), and Brassard (1984a) have suggested the possibility that some Newfoundland bryophytes survived the last glaciation in unglaciated areas of Newfoundland and adjacent areas of the Grand Banks (which would have been land during Wisconsin Glaciations).

Vitt (1970), and Brassard (1983c, 1984b) have suggested that a few bryophytes with disjunctions, particularly from Europe, may have been introduced by man to the Gulf.

Thus, the theories used to explain the presence of disjunct plants in the Gulf of St. Lawrence region have varied from accidental introduction by man, to stepwise dispersal and natural long distance dispersal, to survival in ice-free areas during Wisconsin Glaciations.

Chapter 2

MATERIALS AND METHODS

The disjunct bryophyte species used in this study are those occurring in the study area (Gulf of St. Lawrence) which, (1) in North America, have an 800 km disjunction in the central portion of the continent (Figure 2-1, A), or, (2) show a major disjunction from eastern North America to either eastern Asia or to Europe, or (3) have an arctic-alpine distribution as defined by Schofield (1980).

2.1. Field and Herbarium Studies

The purpose of the field work was to document known sites of disjunct bryophytes or plants, to search for new disjuncts, to fill in gaps of the Gulf distributions of moss and hepatic species, and to become familiar with the ecologies of the bryophyte disjuncts. Field work was conducted over three field seasons (1981-1983).

A total of 207 days were spent investigating ca. 140 sites. These supplemented collecting done in the Gulf by previous workers. Figure 2-2 shows the major localities visited, and also summarizes sites studied by other collectors. Collecting sites in the Maritimes are not shown, but according to R.R. Ireland (personal communication, 1985) about 200 sites have been studied in that region.

Figure 2-1. The disjunctive areas in North America of the Gulf of St. Lawrence bryophytes. A denotes the Arctic; C, central North America; G, Gulf centre; L, Great Lakes; S, southern Appalachians; W, western North America.

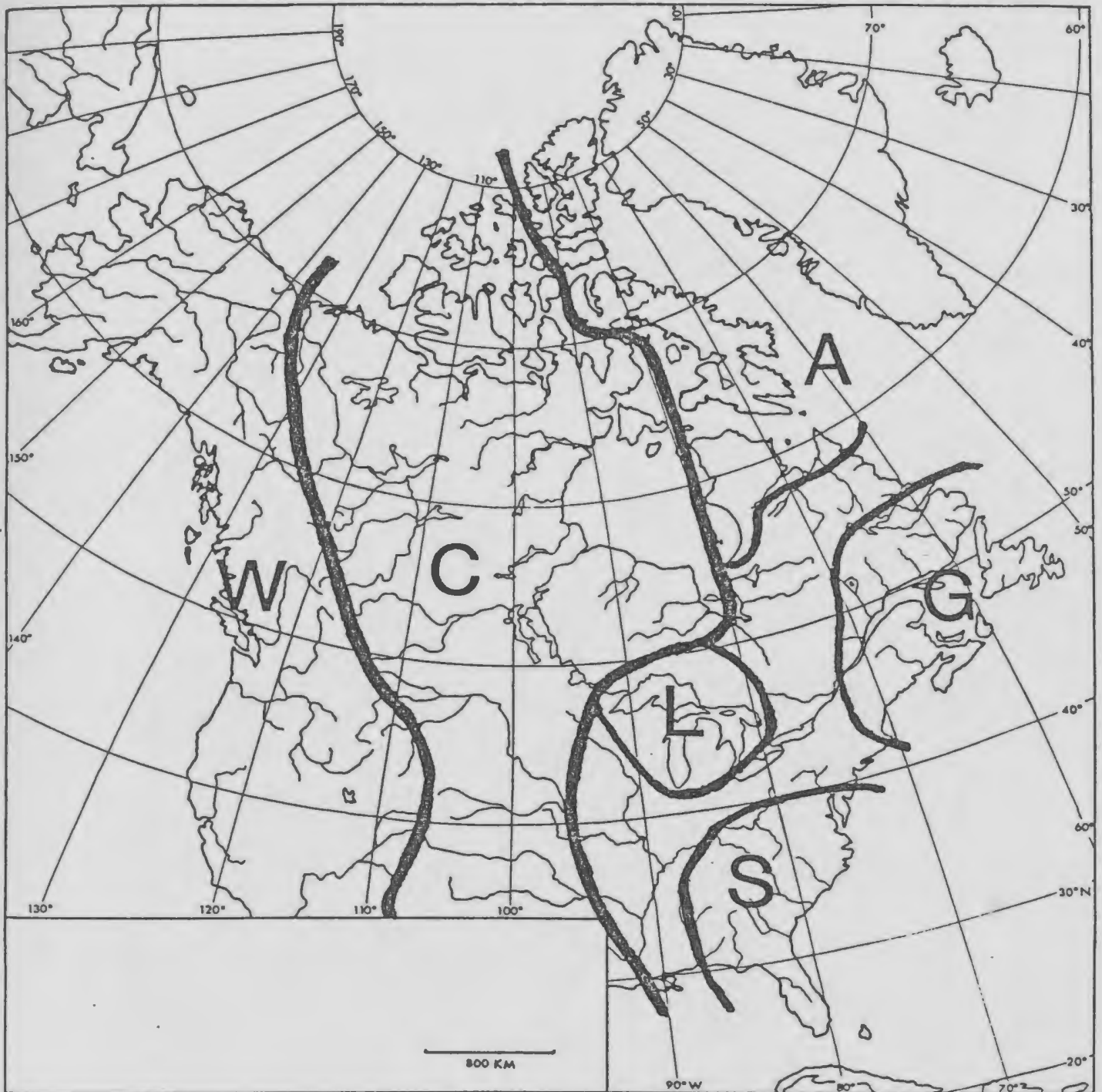
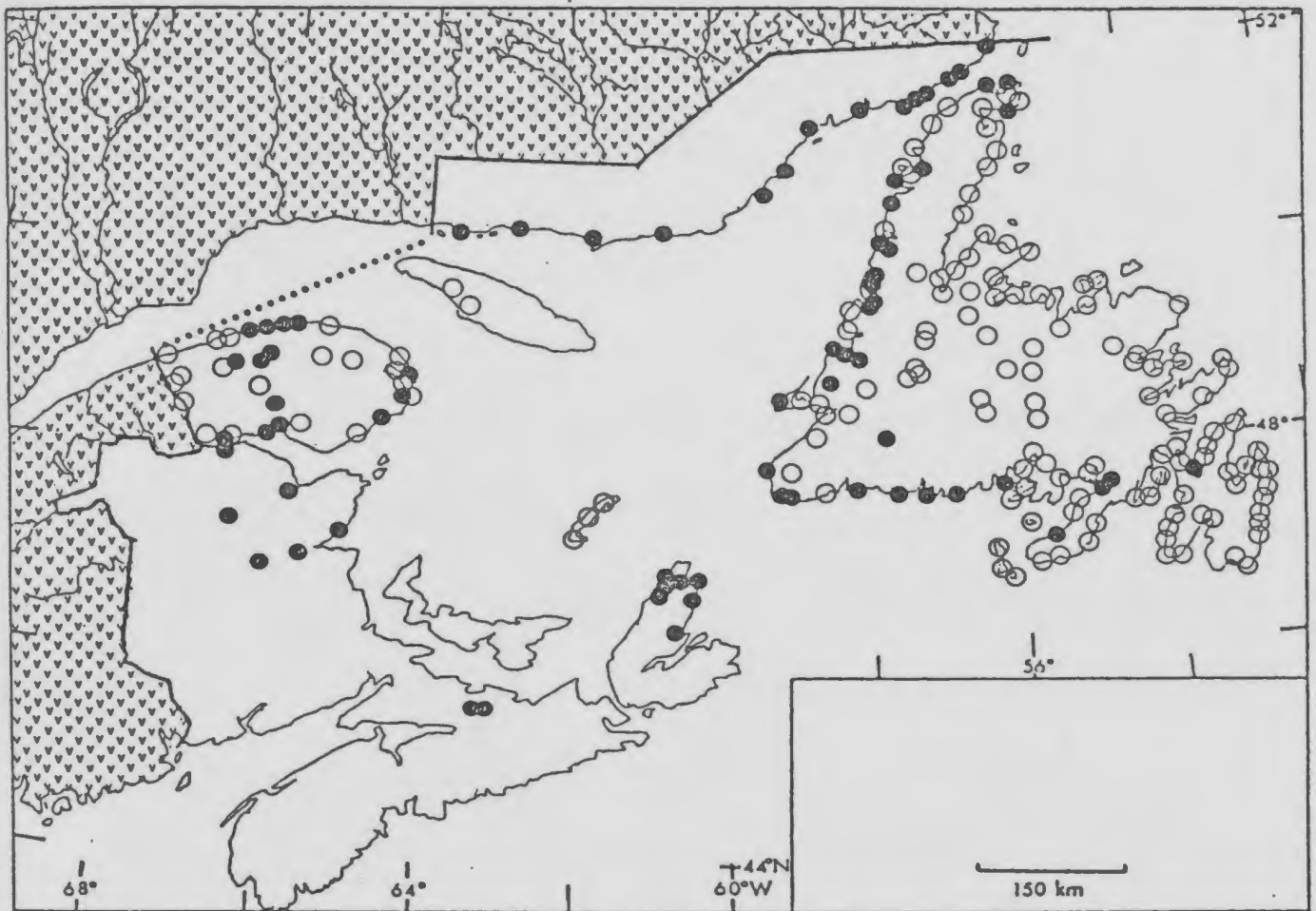


Figure 2-2. Map showing the major collecting sites visited for bryophytes in the Gulf of St. Lawrence. Solid dots indicate major sites studied by the author; circles indicate sites studies by other workers.



Sites for detailed study were chosen for one or more of the following reasons: (1) the site is believed unglaciated during the Wisconsin Glaciation from geomorphological evidence, (2) the site is known to have disjunct and/or endemic plants, (3) the site has a special soil or rock type potentially important to disjunct plants (especially serpentine and limestone), (4) the site has a special habitat (snowbeds, coastal meadows, rich fens, seacliffs, limestone barrens, tundra) of importance to disjunct plants.

At each site, an effort was made to collect all disjunct bryophytes present, and notes were made on the general physiography and vegetation. Approximately 3,000 voucher specimens were collected; the main set of these is deposited at the Bryological Herbarium of Memorial University, St. John's (NFLD).

Lists of the disjuncts were compiled, and maps were made using all available distributional data, including literature reports, herbarium records, and my own collections. Particularly important sources of North American bryophyte distributions were Schofield (1969, 1972, 1980), Schofield and Crum (1972), Crum and Anderson (1981), and Schuster (1966, 1969, 1974, 1980). Previously published maps (sources mainly from Sjödin 1980a, 1980b) were also compiled. Many additional sources for distributional data such as recent taxonomic revisions and checklists were also used (see Appendix A for a complete list of the major sources).

In order to make phytogeographic comparisons, a conservative species concept is necessary; therefore the number of species treated here is somewhat lower than found in other sources. The taxonomy used generally follows Crum *et al.* (1973) for the mosses, and Schuster (1966, 1969, 1974, 1980) for the hepatics. Stotler and Crandall-Stotler (1977) is used for the hepatics not found in Schuster's volumes. Generic concepts in some families (notably Mniaceae, Polytrichaceae, and Grimmiaceae) follow recent taxonomic revisions (Koponen 1968; Smith 1971; Bremer 1980a, 1980b, 1981).

The non-disjunct bryophytes referred to in this study include all those present in the Gulf study area. Lists of these were compiled from Brassard (1983b), Brassard and Williams (1975), Crum and Anderson (1981), Ireland (1982), and Schuster (1966, 1969, 1974, 1980), as well as from my own collections and those of others not yet published.

2.2. Analyses

The analyses were completed in three major parts as follows:

(1) grouping of the Gulf of St. Lawrence disjunct bryophyte species into sub-elements with similar distributions in eastern North America,

(2) assignment of the sub-elements to the most likely of six possible migrational/dispersal explanations:

i) Postglacial long distance dispersal

a) natural

b) introduction by man

ii) Postglacial migration to the Gulf

a) from the south

b) from the north

c) from western North America along a tundra
corridor

iii) Survival in ice-free areas in the Gulf region

during the Wisconsin Glaciation

(3) examination of the Gulf of St. Lawrence distributions of groups best supporting each of the six explanations for common relationships.

2.2.1. Grouping species into sub-elements

The first analysis involved grouping disjunct bryophytes based on the similarity of their distributions in eastern North America. Species with similar eastern North American distributions were assumed more likely to have had a similar recent migrational or dispersal history to the Gulf.

Since the majority of the disjuncts were not strictly limited to the study area a larger "Gulf centre" was defined, whose limits extended north to

Hopedale/Schefferville (55°N), west to Quebec City and south to Cape Cod (Massachusetts), although the detailed analyses were confined to the study area (Figure 1-1, page 3). To avoid confusion between the two, the term "Gulf centre" will be used only in reference to the larger centre, and other terms (e.g., 'Gulf of St. Lawrence', and 'Gulf') will refer to the study area.

The disjunct bryophytes have varying degrees of continuity or discontinuity from the Gulf centre to three other main regions of eastern North America: the Arctic (north of treeline), the Southern Appalachians (the Appalachian Mountains and Coastal Plain south of Virginia), and the western Great Lakes (Huron, Michigan, Superior,) (Figure 2-1). A species was considered disjunct from the Gulf to one of those three regions only if the closest population in the Gulf centre was farther than 800 km from the population in or nearest these regions. A diagrammatic scheme was devised to show the continuity or discontinuity of sub-elements from the Gulf centre to the other three centres (see Figure 3-1, page 48).

I was not able to confirm, by field investigation, the presence or absence of bryophyte disjuncts between the Gulf centre and any of the three other centres defined above. However, field work and publications by others has been sufficient to indicate the presence/absence of species in the intervening areas, e.g., (1) southern Quebec-Ontario (Lepage 1943, 1944, 1945, 1946; Schuster 1966, 1969, 1974, 1980; Ireland and Cain 1975), (2) New England (Hafferty 1960; Ketchledge

1980; Crum and Anderson 1981), (3) central Labrador (Brassard and Williams 1975; Brassard and Webr 1976; Ireland *et al.* 1980; many unpublished records deposited in NFLD).

2.2.2. Assignment of sub-elements to migrational/dispersal hypotheses

If the eastern North American patterns of distribution resulted from several different glacial and post-glacial migrational and dispersal histories to the Gulf region, then there should be distinct relationships between these distribution patterns and each of the six possible migrational/dispersal histories. The present analysis determined which of the six explanations (summarized earlier, page 34) best fit how the species in each sub-element reached the Gulf of St. Lawrence region based on present-day distribution.

1. *Postglacial Long Distance Dispersal to the Gulf*

a) Naturally

Sub-elements containing species most likely to have reached the Gulf via long distance dispersal in postglacial time ought to show distributions in eastern North America in which (1) the sub-element has its only eastern North American centre in the Gulf of St. Lawrence, or (2) if other populations are present elsewhere in eastern North America, then the Gulf populations are disjunctive to these also.

In addition, sub-elements supporting long distance dispersal would be expected to comprise species that are better adapted for such dispersal than species which are less well adapted.

This hypothesis was tested for both mosses and hepatics with a chi-squared 2-way contingency table (Sokal and Rohlf 1969) analysis for independence using diaspore size as a measure of dispersal potential and distribution type.

Dispersal potential was based on the supposition that dispersal distance decreases with increasing diaspore size (Schmidt 1918). Van Zanten and Pócs (1980) have suggested long distance dispersal as feasible only if diaspores are smaller than 25 μm . Two diaspore classes were defined using this figure as a limit. The classes are defined below and reflect decreasing potential for long distance dispersal:

1. High. $<25 \mu\text{m}$ (spores, gemmae)
2. Low. $>25 \mu\text{m}$ (spores, gemmae, fragile gametophyte fragments, brood bodies, or no known sexual or obvious asexual propagules)

Spore sizes were used to class most species. When the spore size range spanned a size class boundary, the species was assigned to the smaller class. Diaspore size data was obtained mainly from Arnell (1954), Nyholm (1954-1969), Schuster (1966, 1969, 1974, 1980), Lawton (1971), and Crum and Anderson (1981).

The distribution types were disjuncts and non-disjuncts. The disjuncts included all species in sub-elements most likely to have reached the Gulf via long distance dispersal (outlined above), and the non-disjuncts were those species with continuous distributions to the Gulf.

b. Introductions by man

Bryophytes in sub-elements best supporting the hypothesis of introduction by man to the Gulf will have distributions in eastern North America centred on this region (see Lindroth 1957; Brassard 1983b, 1983c). Therefore, sub-elements containing species that were introduced to this region by man will have the Gulf as the only centre of distribution in eastern North America.

2. *Postglacial Migration to the Gulf of St. Lawrence*

a. From areas south of the Gulf

If a large proportion of the species within a sub-element migrated to the Gulf from the south postglacially, then their distributions should show a continuity between the Gulf and the region south of the Gulf centre.

b. From areas north of the Gulf

If a large proportion of the species within a sub-element migrated to the Gulf from the north postglacially, then their distributions would be centred in Arctic regions, and would show continuity between the Gulf and this area.

c. From western North America along a tundra corridor or survival in a tundra corridor

If the bryophytes within a sub-element migrated to the Gulf postglacially from western North America along a tundra corridor, or survived in a tundra corridor during glaciation, then one expects (1) these species to have intermediate stations between western North America and eastern North America at the Great Lakes where some tundra habitats also persist, (2) the species to be absent between the Gulf region and the Great Lakes since no tundra is presently found there, and, (3) the species to be in the Arctic today, since they are primarily tundra species. Such species might also be present as relics in the southern Appalachians, but then they would most likely show a disjunction from the Gulf to the southern Appalachians.

3. Survival in ice-free refugia in the Gulf of St.

Lawrence Region during the Wisconsin Glaciation

If species in a sub-element survived the Wisconsin Glaciation in the Gulf they are most likely well adapted for survival in a tundra environment such as might have existed in Gulf ice-free areas. Most such species are today likely found in the Arctic. While unlikely that many species with southern affinities could have existed under refugial conditions, it has been suggested that non-arctic

plant species might have survived glaciation on the Grand Banks, and that climates in such coastal refugia may have been relatively mild (Lindroth 1970; Morriset 1971; Brassard 1984a). Therefore, species not necessarily well adapted to harsh environments must also be considered as possible refugial candidates.

Glaciation would have undoubtedly disrupted formerly more continuous ranges. Thus, species best supporting a refugial hypothesis would have geographically isolated populations in the Gulf region. These may represent the only populations of the species in eastern North America, or if other populations are present in eastern North America, then the Gulf populations would be disjunct from them.

Sub-elements were assigned to a history based on the above hypotheses. If the evidence was not clear, then a sub-element was assigned to the two most likely hypotheses.

2.2.3. The Gulf of St. Lawrence distributions of species within groups supporting given migrational/dispersal histories

More than one sub-element may support a given migrational/dispersal history. The distributions of species contained in all sub-elements supporting a given migrational/dispersal history are expected to show similarities in some aspects of their Gulf of St. Lawrence distribution. Two aspects are examined in this analysis: (1) frequency of disjunct species within the Gulf, and (2) centres of diversity of disjunct species within the Gulf region.

To make comparisons of species distributions, the study area was divided into 17 regions (Figure 2-3) based on the following criteria: (1) that contiguous land regions have about the same area, (2) that these regions be not so small as to be undercollected, and, (3) that all regions have coastline and therefore some maritime influence. Naturally delimited areas such as islands were considered as separate regions.

(1) *Frequency of occurrence in the Gulf of St. Lawrence.*

A relative frequency scale was used for occurrences in the Gulf of St. Lawrence (Table 2-1).

(2) *Diversity within the Gulf of St. Lawrence*

For each migrational/dispersal history, the diversity of the disjuncts was analysed for each region in the Gulf of St. Lawrence (Figure 2-3).

Figure 2-3. The Gulf of St. Lawrence regions used for floristic comparisons. ANT denotes Anticosti Island; FE, eastern Newfoundland; FNE, northeastern Newfoundland; FNW, northwestern Newfoundland; FS, Newfoundland south coast; FSW, southwest Newfoundland; GAS, Gaspé Peninsula; MDI, Magdalen Islands; NBC, central New Brunswick; NBN; northern New Brunswick; NBS, southern New Brunswick; NOE, southern Labrador; NOW, Quebec North Shore; NSC, central Nova Scotia; NSN, northern Nova Scotia; NSS, southern Nova Scotia; PEI, Prince Edward Island.



Table 2-1. Relative frequency scale used for disjunct bryophyte occurrence in the Gulf of St Lawrence.

Relative frequency	Number of Gulf regions in which the species occurs
(1) very rare	1
(2) rare	2-4
(3) occasional	5-9
(4) common	10-13
(5) very common	14-17

Chapter 3

RESULTS

One hundred-ninety-nine mosses and 68 hepatics have disjunct distributions from the Gulf of St. Lawrence to other regions of North America, Europe, or Asia. The disjunct bryophytes comprise 38% of the 698 species (526 mosses, 172 hepatics) of the bryophytes of the study area.

Field work resulted in the addition of many bryophyte species to the Gulf of St. Lawrence flora. One species *Trematodon montanus* Belland and Brassard, was described new to science. Other critical bryophytes added to the Gulf flora include: *Andreaea blyttii*, *Andreaea nivalis*, *Brachythecium collinum*, *Dicranum acutifolium*, *Grimmia atrata*, *Grimmia donniana*, *Grimmia incurva*, *Gymnomitrion corralioides*, *Kiaeria falcata*, *Kiaeria glacialis*, *Lescureae saxicola*, *Marsupella condensata*, *Moerckia blyttii*, *Myurella tenerrima*, *Oedipodium griffithianum*, *Orthothecium chryseum*, *Pohlia obtusifolia*, *Polytrichastrum sexangulare*, *Scapania crassiretis*, *Scapania hyperborea*, *Scapania uliginosa*, *Schistidium trichodon*, and *Tortella arctica*.

In addition, an entire and distinct community of disjunct bryophytes, the late-snowbed community, was discovered and described for the first time in eastern North America.

My field work added new records of species for many regions of the Gulf. Most of these have been included in Appendix A. Among the more important records include (abbreviations for regions in Appendix A): *Aongstroemia longipes* (sL), *Arctoa fulvella* (M), *Aulacomnium turgidum* (Nf), *Bartramia ithyphylla* (M), *Campyllum halleri* (Qns), *Encalypta longicolla* (Qns), *Entodon concinnus*, *Marsupella sparsifolia* (Nf), *Metacalypogeia schusterana* (Qns), *Orthothecium strictum* (Ga, Qns), *Orthotrichum alpestre* (sL), *Pleuroclada albescens* (Nf), *Pseudoleskea patens* (Ga), *Seligeria donniana* (M), *Seligeria tristichoides* (M), *Timmia norvegica* (Ga, M), *Zygodon viridissimus* (Ga, Qns).

3.1. Assignment of Species to Sub-elements

Based on their continuity or discontinuity in eastern North America (as outlined in section on page 37), the disjuncts fell into 22 (of a possible 27) sub-elements (Figure 3-1, Table 3-1). The species in each sub-element and their presence in the regions of the study area are given in Appendix B. The eastern North American distributions of the sub-elements are represented diagrammatically in Figure 3-1.

3.2. Assignment of Sub-elements to Migrational/Dispersal Hypotheses

The sub-elements of the Gulf of St. Lawrence disjuncts were found to support five different migrational/dispersal histories (Table 3-2). Most sub-

Figure 3-1. Diagrammatic representation of the bryophyte sub-elements in the Gulf of St. Lawrence. Letters refer to regions shown in Figure 2-1: A, Arctic; G, Gulf of St. Lawrence; L, Great Lakes; S, Southern Appalachians. Continuous lines joining two regions indicate a continuous distribution between them; dotted lines indicate a disjunction.

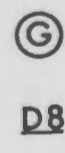
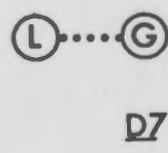
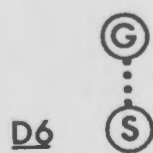
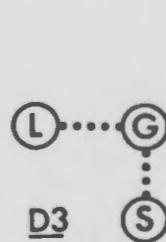
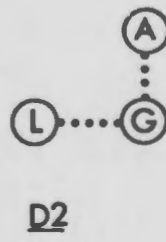
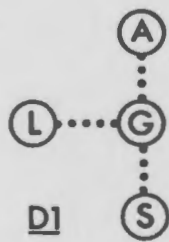
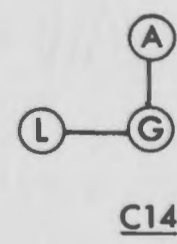
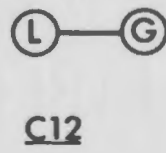
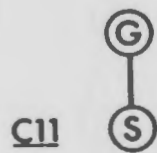
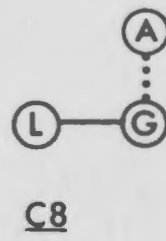
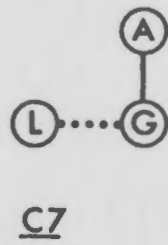
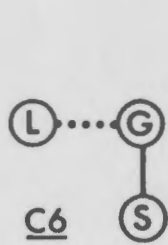
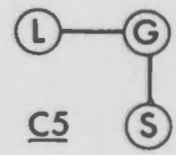
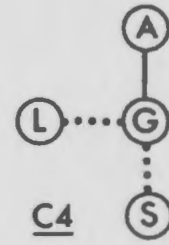
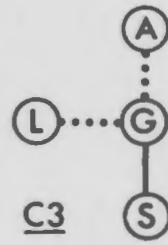
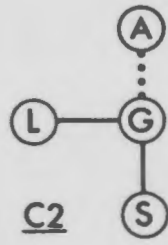
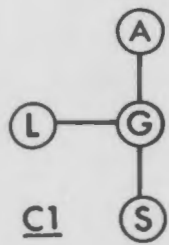


Table 3-1. The bryophyte sub-elements in the Gulf of St. Lawrence.

Sub-element (Fig. 3-1)	no. of mosses	% of total moss disjuncts	no. of hepatics	% of total hepatic disjuncts
<hr/>				
C1	4	2.0	3	4.4
C2	20	10.0	1	1.5
C3	2	1.0	0	0.0
C4	1	0.5	2	2.9
C5	32	16.0	5	7.4
C6	1	0.5	2	2.9
C7	9	4.5	4	5.9
C8	5	2.5	3	4.4
C9	4	2.0	0	0.0
C10	20	10.0	4	5.9
C11	4	2.0	1	1.5
C12	1	0.5	3	4.4
C13	1	0.5	0	0.0
C14	2	1.0	0	0.0
D1	3	1.5	1	1.5
D2	14	7.0	14	20.6
D3	3	1.5	0	0.0
D4	1	0.5	1	1.5
D5	42	21.1	19	27.9
D6	7	3.5	1	1.5
D7	5	2.5	2	2.9
D8	18	9.0	2	2.9
<hr/>				
Total	199	99.6	68	100.0

elements (containing 74% of the disjunct bryoflora) support only one history, but 68 species in five sub-elements (C4, C7, D1, D2, D8) have eastern North American distributions which did not allow unequivocal assignment to a single history and these five sub-elements are listed under each of two histories in Table 3-2. No disjunct bryophytes whose eastern North American distribution might support long-range dispersal had diaspore sizes which might support this hypothesis (see Appendix C). Only two sub-elements could not be assigned to any migrational/dispersal history. In all, six migrational/dispersal bryophyte groups (supporting five histories or combination of histories) were analysed (Tables 3-3 to 3-7) based on presence in other eastern North American centres (arctic, Great Lakes, southern Appalachians). Species which survived in refugia and/or were introduced to the study area (sub-element D8 only) do not occur in any Eastern North American centre other than the Gulf.

Table 3-2. Summary of sub-elements supporting six possible migrational/dispersal hypotheses to the Gulf of St. Lawrence.

History	Sub-elements	Total species	
		Mosses	Hepatics
Introductions			
by Man	D8	18	2
Natural Long			
Distance Dispersal	NONE	NONE	NONE
Migration from the			
South	C1, C2, C3, C5, C6, C9, C11, C13	68	12
Migration from the	C4, C7, C10, C14	30	10
North			
Migration from the	C4, C7, D1, D2	27	21
West			
Survival in Refugia	D1, D2, D3, D4, D5, D6, D7, D8	93	40
Unexplained	C8, C12	6	6

Table 3-3. Eastern North American occurrence of bryophytes which support migration to the Gulf of St. Lawrence from the south.

	Total	Arctic		Great Lakes		S. Appalachians	
	Species	no.	%	no.	%	no.	%
Mosses	68	31	46	59	87	68	100
Hepatics	12	4	33	11	92	12	100
Total	80	35	44	70	88	80	100

Table 3-4. Eastern North American occurrence of bryophytes which support migration to the Gulf of St. Lawrence from the north.

	Total	Arctic		Great Lakes		S. Appalachians	
	Species	no.	%	no.	%	no.	%
Mosses	22	22	100	2	9	0	0
Hepatics	4	4	100	0	0	0	0
Total	26	26	100	2	8	0	0

Table 3-5. Eastern North American occurrence of bryophytes which support migration to the Gulf of St. Lawrence from the north and/or west (sub-elements C4 and C7).

	Total	Arctic		Great Lakes		S. Appalachians	
	Species	no.	%	no.	%	no.	%
Mosses	10	10	100	10	100	1	10
Hepatics	6	6	100	6	100	2	33
Total	16	16	100	16	100	3	19

Table 3-6. Eastern North American occurrence of bryophytes which support survival in refugia or migration to the Gulf of St. Lawrence from the west (sub-elements D1 and D2).

	Total	Arctic		Great Lakes		S. Appalachians	
	Species	no.	%	no.	%	no.	%
Mosses	17	17	100	17	100	3	18
Hepatics	15	15	100	15	100	1	7
Total	32	32	100	32	100	4	13

Table 3-7. Eastern North American occurrence of bryophytes which support survival in refugia in the Gulf of St. Lawrence.

	Total	Arctic		Great Lakes		S. Appalachians	
	Species	no.	%	no.	%	no.	%
Mosses	58	43	74	8	14	12	21
Hepatics	23	18	78	2	9	2	9
Total	81	61	75	10	12	14	17

3.3. The Gulf of St. Lawrence Distributions of Species Within Groups Supporting Migrational/Dispersal Histories

Frequency

Tables 3-8 to 3-13 show the frequencies in the Gulf of species supporting each history or combination of histories.

Diversity

Table 3-14 summarizes the numbers of disjunct and non-disjunct bryophytes in each region of the study area. Table 3-15 summarizes the numbers of disjuncts in each region for each migrational/dispersal history, or combination of histories. Figures 3-2 to 3-12 show the regional diversities of the disjuncts as percentages of the total species supporting each history or combination of histories.

Table 3-8. Frequency within the Gulf of St. Lawrence of bryophytes which migrated from the south.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	3	4	1	8	5
rare	11	16	2	17	16
occasional	27	40	4	33	39
common	15	22	3	25	23
very common	12	18	2	17	18
Total	68	100	12	100	101

Table 3-9. Frequency within the Gulf of St. Lawrence of bryophytes which migrated from the north.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	3	14	1	25	15
rare	10	45	1	25	42
occasional	7	32	2	50	35
common	2	9	0	0	8
very common	0	0	0	0	0
Total	22	99	4	100	100

Table 3-10. Frequency within the Gulf of St. Lawrence of bryophytes which migrated from the north and/or west.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	1	10	1	17	13
rare	5	50	1	17	38
occasional	3	30	4	67	44
common	1	10	0	0	6
very common	0	0	0	0	0
Total	10	100	6	101	101

Table 3-11. Frequency within the Gulf of St. Lawrence of bryophytes which survived in refugia or migrated from the west.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	5	29	5	33	31
rare	9	53	6	40	47
occasional	2	12	3	20	16
common	1	6	1	7	6
very common	0	0	0	0	0
Total	17	100	15	100	100

Table 3-12. Frequency within the Gulf of St. Lawrence of bryophytes which were introduced or survived in refugia.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	7	39	0	0	35
rare	6	33	2	100	40
occasional	3	17	0	0	15
common	2	11	0	0	10
very common	0	0	0	0	0
Total	18	100	2	100	100

Table 3-13. Frequency within the Gulf of St. Lawrence of bryophytes which survived in refugia.

Frequency	no. of mosses	% of mosses	no. of hepatics	% of hepatics	average %
very rare	22	38	7	30	36
rare	24	41	12	52	44
occasional	11	19	2	9	16
common	1	2	2	9	4
very common	0	0	0	0	0
Total	58	100	23	101	100

Table 3-14. Total numbers of disjunct and non-disjunct bryophytes in the Gulf of St. Lawrence.

Region	Total Disjunct Flora		Total Non-Disjunct Flora		Total Flora	
	Mosses	Hepatics	Mosses	Hepatics	Mosses	Hepatics
ANT	21	5	74	10	95	15
FE	75	28	196	67	271	92
FNE	65	18	186	52	251	70
FNW	130	44	220	55	350	99
FS	51	24	148	55	199	79
FSW	97	38	210	64	307	102
GAS	103	49	226	56	329	105
MDI	19	2	106	14	125	16
NBC	38	5	149	16	187	21
NBN	48	6	185	7	233	13
NBS	66	8	211	27	277	35
NOE	53	9	122	16	175	25
NOW	36	11	118	33	154	44
NSC	63	16	210	53	273	69
NSN	76	36	217	68	293	104
NSS	66	9	196	33	262	42
PEI	35	4	131	18	166	22

Table 3-15. Regional bryophyte diversity (numbers of species) in the Gulf of St. Lawrence for six migrational/dispersal histories. M, mosses; H, hepatics. Histories: 1, Introductions/Refugia; 2, Migration from South; 3, Migration from North and/or West; 4, Migration from West and/or Refugia; 5, Migration from North; 6, Survival in Refugia.

Region	History											
	1		2		3		4		5		6	
	M	H	M	H	M	H	M	H	M	H	M	H
ANT	3	0	9	4	2	0	1	0	5	0	1	0
FE	10	0	37	8	4	1	2	5	3	1	16	6
FNE	5	0	34	7	4	3	6	3	7	0	7	3
FNW	10	0	39	7	8	5	10	10	22	4	37	14
FS	4	0	30	9	1	2	2	3	3	1	8	6
FSW	10	1	45	10	4	2	7	7	8	1	20	11
GAS	6	0	39	9	6	6	8	9	17	3	24	17
MDI	1	0	14	2	1	0	0	0	1	0	2	0
NBC	0	1	33	4	0	0	1	0	0	0	2	1
NBN	3	1	33	2	2	2	1	2	2	0	3	11
NBS	2	0	50	4	1	0	3	0	2	0	4	3
NOE	2	0	17	3	6	1	2	1	13	1	12	3
NOW	3	1	17	4	3	2	2	3	5	0	4	1
NSC	3	0	47	7	1	2	2	2	3	0	5	4
NSN	5	0	48	10	2	3	2	7	4	0	11	0
NSS	3	0	51	6	1	1	2	0	1	0	5	1
PEI	2	0	25	4	1	0	1	0	1	0	1	0

Figure 3-2. The percentage of the 68 mosses which migrated from the south that occur in the Gulf of St. Lawrence regions.

Figure 3-3. The percentage of the 12 hepatics which migrated from the south that occur in the Gulf of St. Lawrence regions.

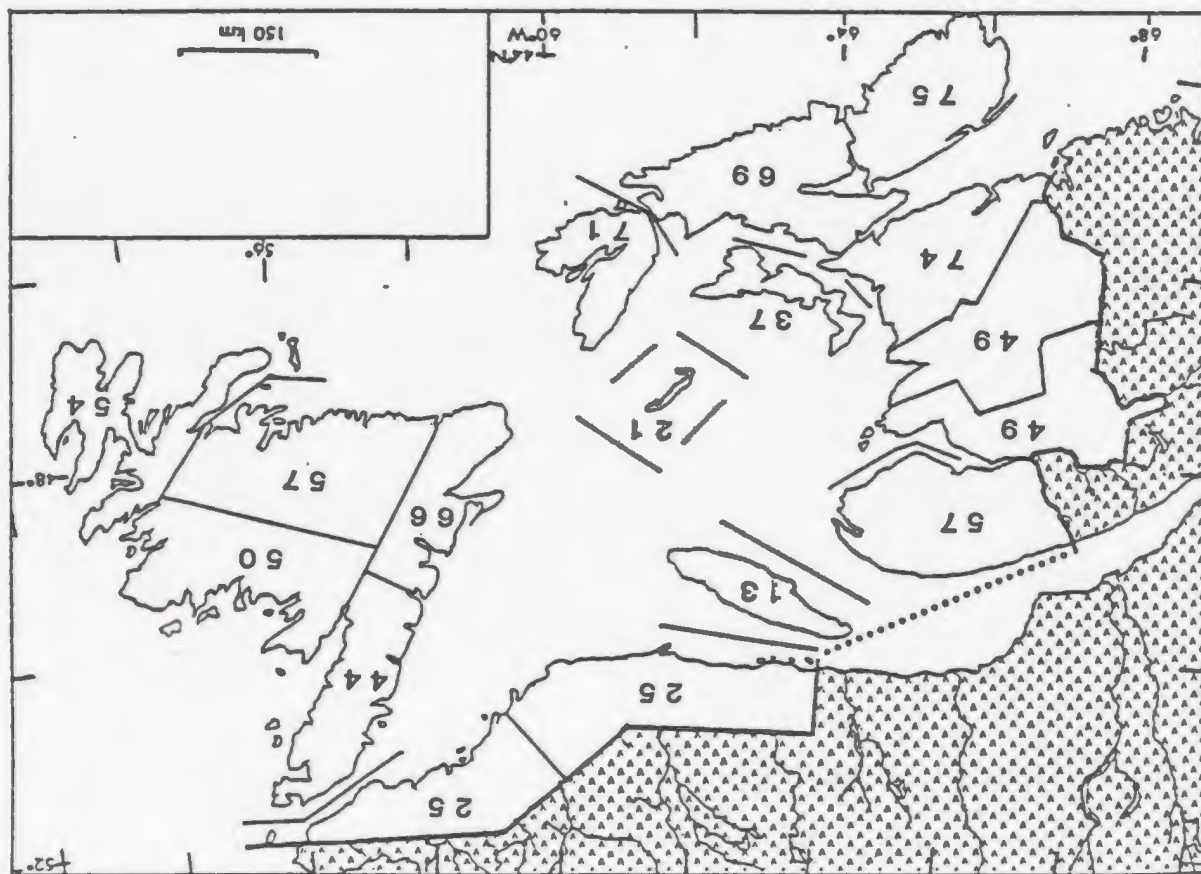
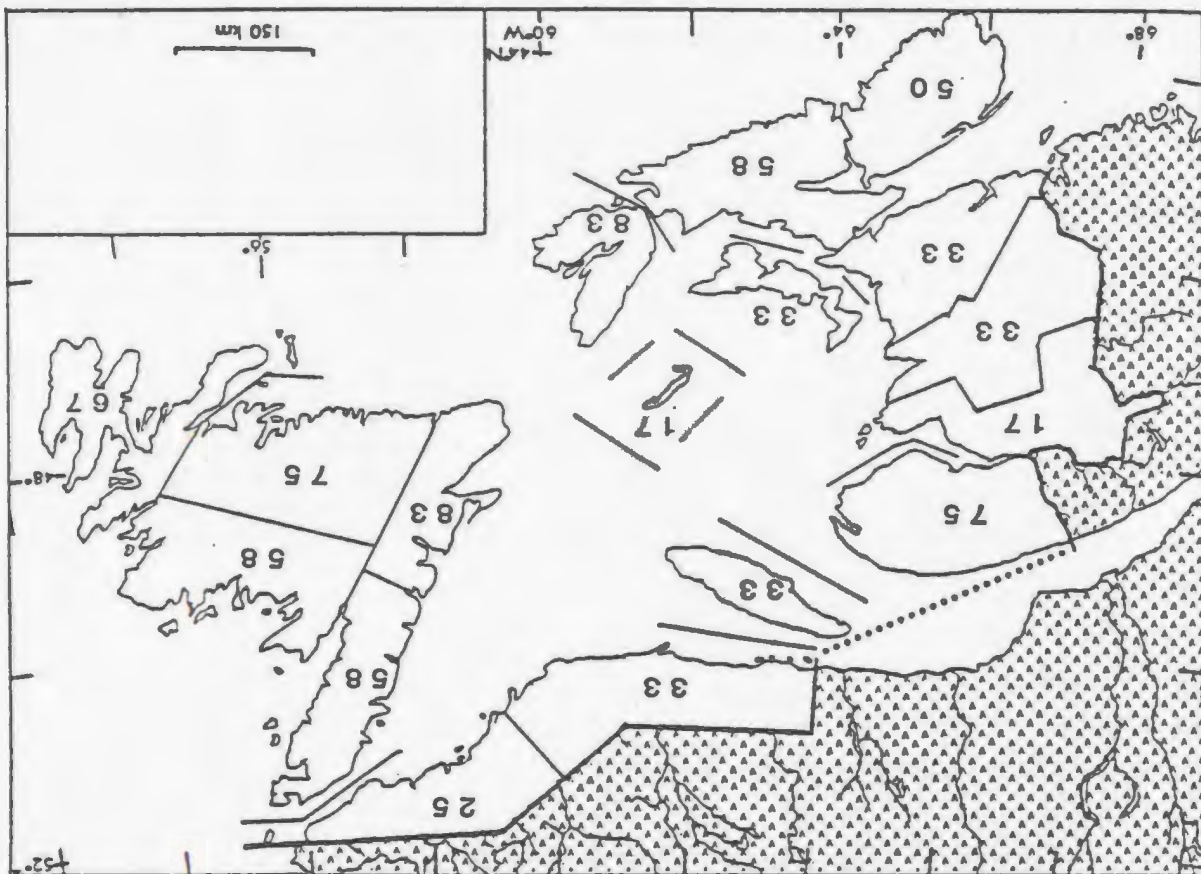


Figure 3-4. The percentage of the 22 mosses which migrated from the north that occur in the Gulf of St. Lawrence regions.

Figure 3-5. The percentage of the 4 hepatics which migrated from the north that occur in the Gulf of St. Lawrence regions.

Figure 3-6. The percentage of the 10 mosses which migrated from the north and/or west that occur in the Gulf of St. Lawrence regions.

Figure 3-7. The percentage of the 6 hepatics which migrated from the north and/or west that occur in the Gulf of St. Lawrence regions.

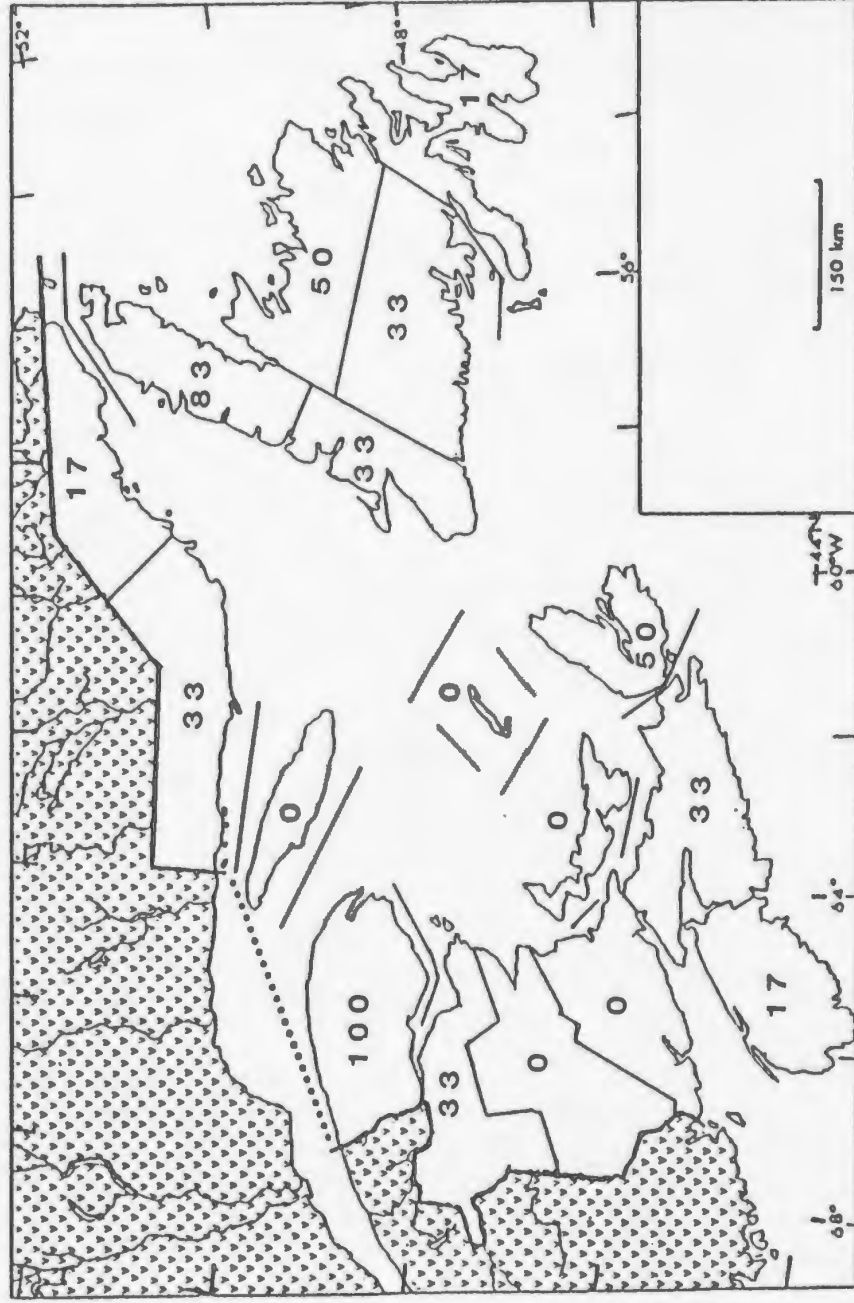
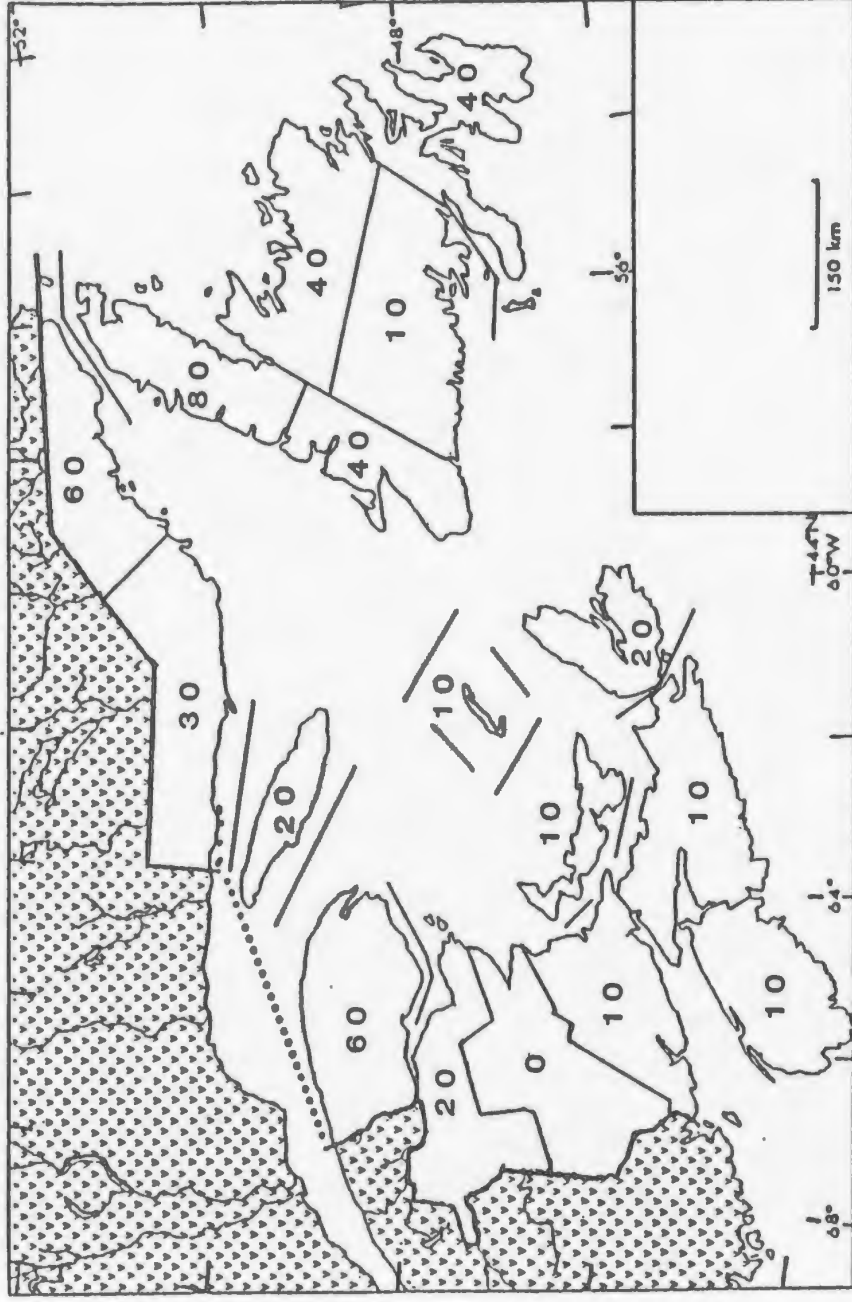


Figure 3-8. The percentage of the 17 mosses which migrated from the west and/or survived in refugia that occur in the Gulf of St. Lawrence regions.

Figure 3-9. The percentage of the 15 hepatics which migrated from the west and/or survived in refugia that occur in the Gulf of St. Lawrence regions.

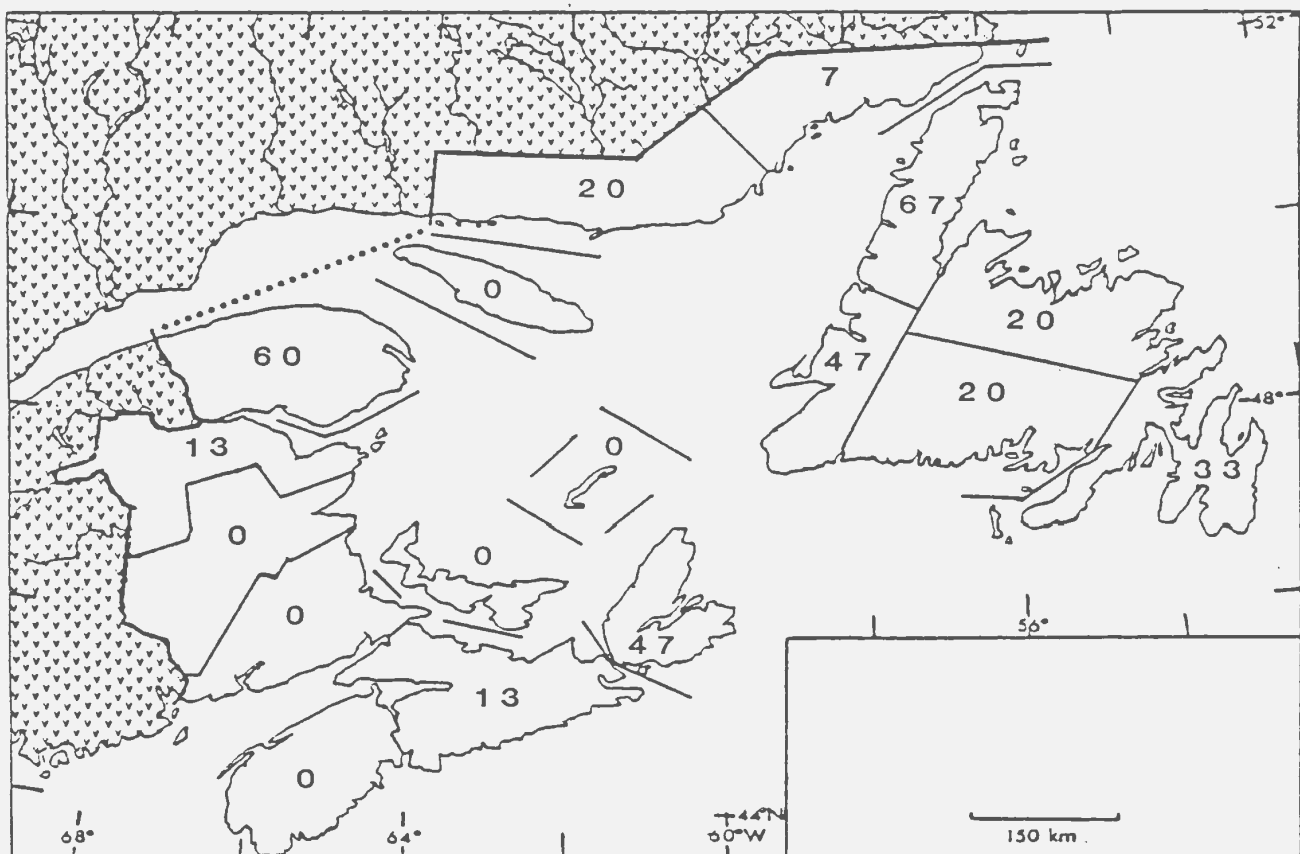
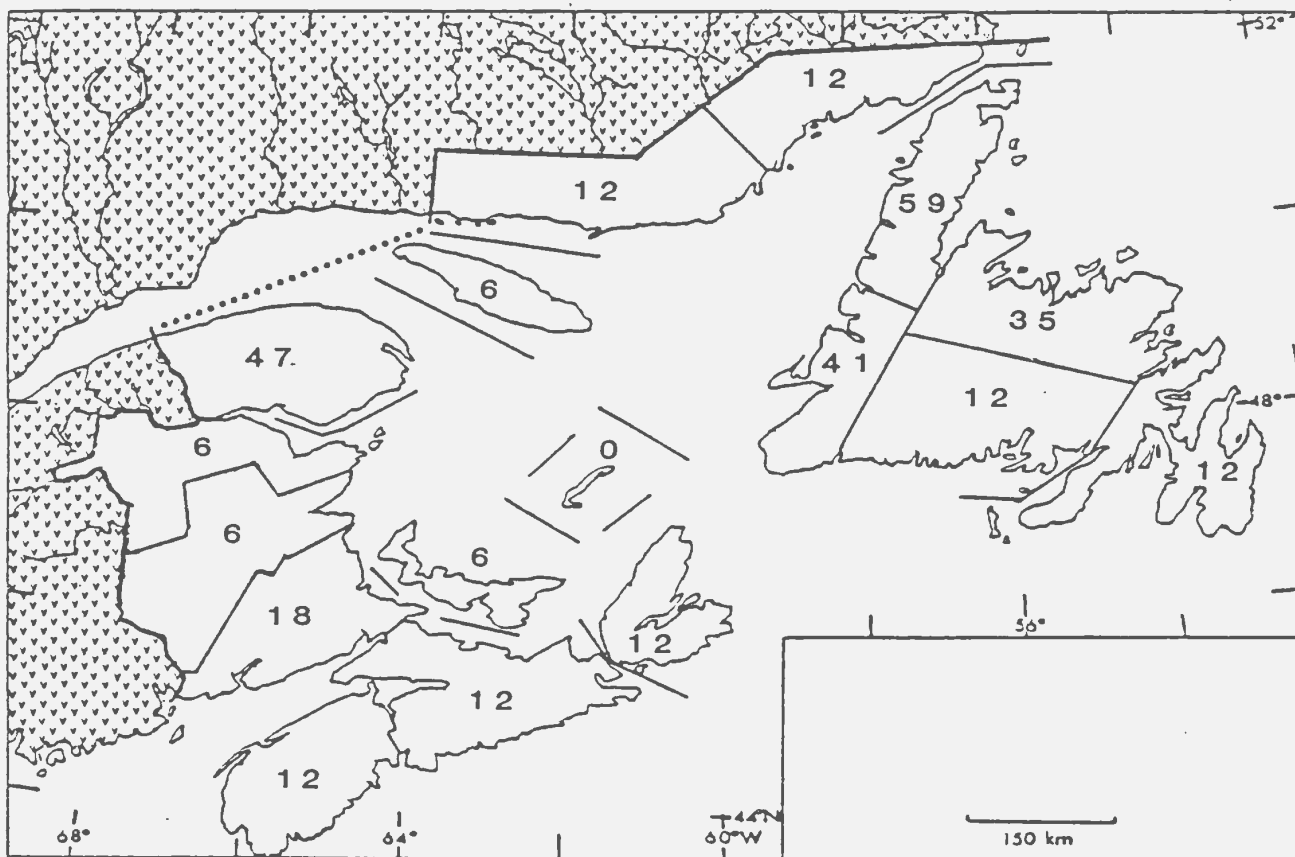
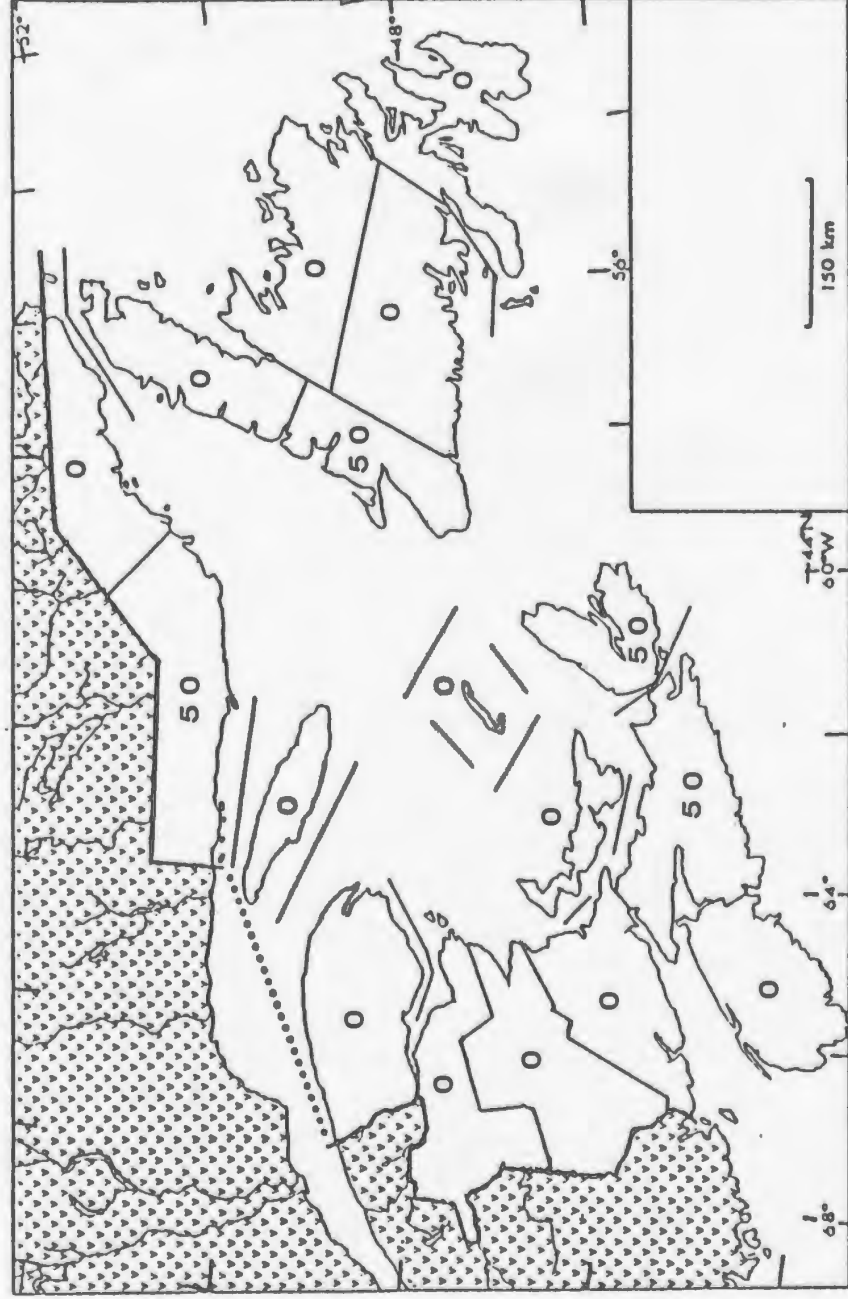
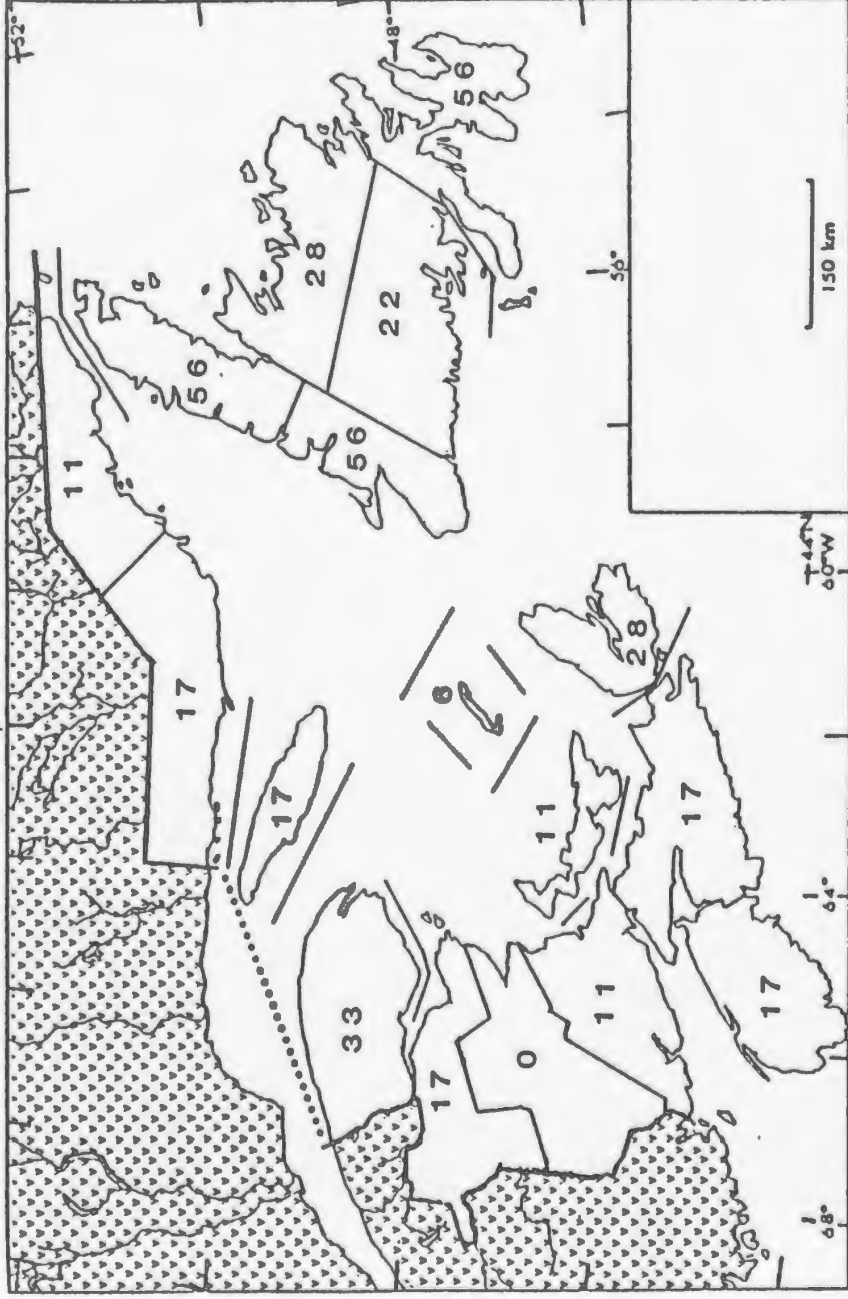


Figure 3-10. The percentage of the 18 mosses which may been introduced or survived in refugia that occur in the Gulf of St. Lawrence regions.

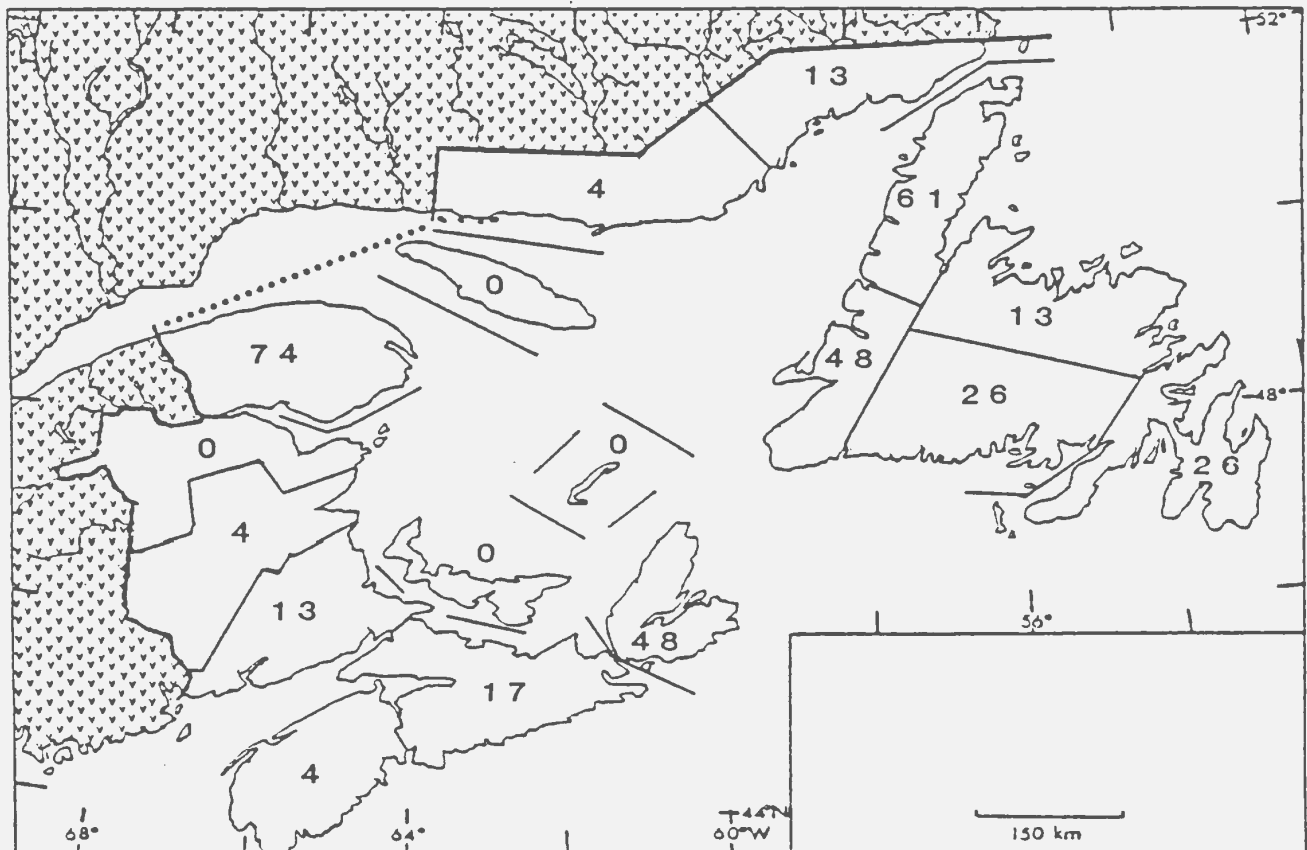
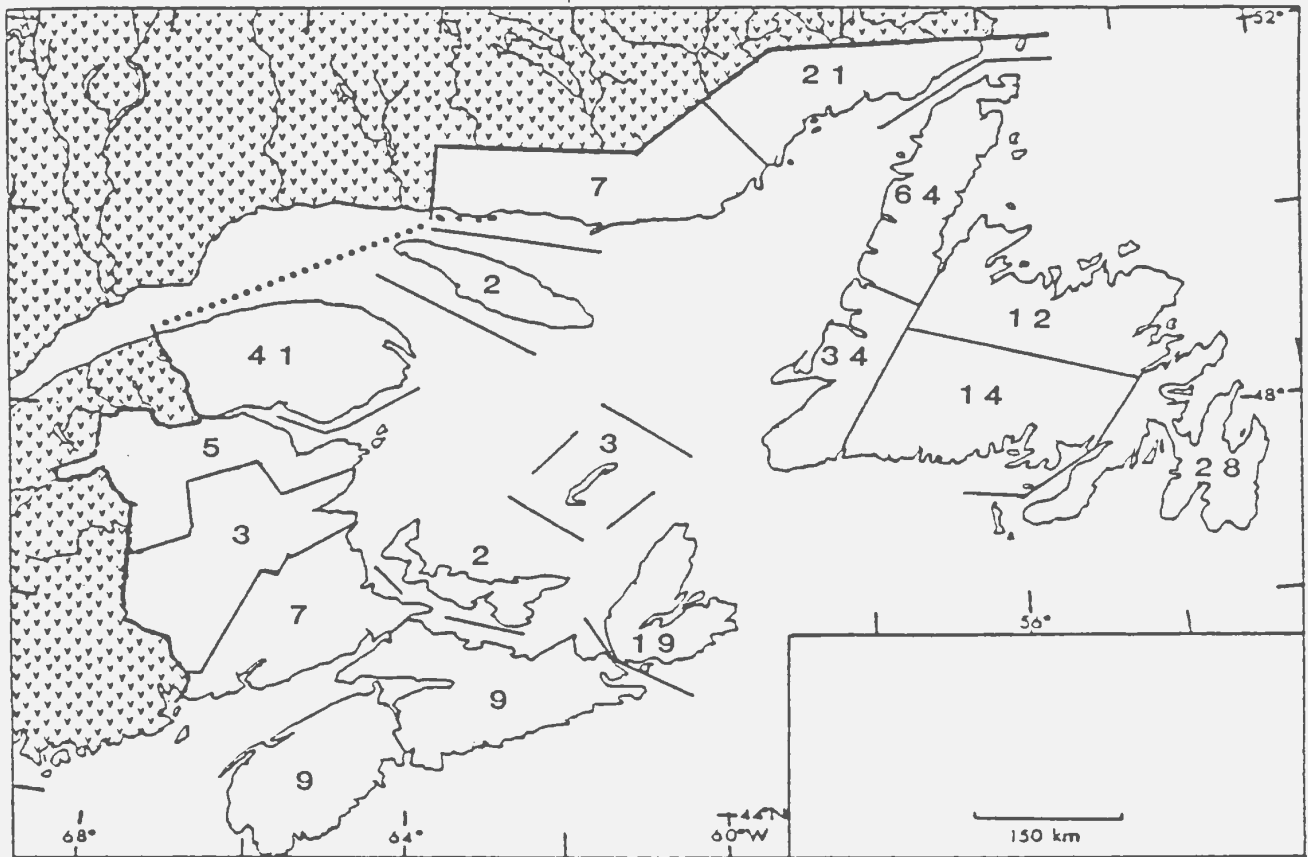
Figure 3-11. The percentage of the 2 hepatics which may been introduced or survived in refugia that occur in the Gulf of St. Lawrence regions.



57

Figure 3-12. The percentage of the 58 mosses which survived in refugia that occur in the Gulf of St. Lawrence regions.

Figure 3-13. The percentage of the 23 hepatics which survived in refugia that occur in the Gulf of St. Lawrence regions.



Chapter 4

DISCUSSION

4.1. Gulf of St. Lawrence Distributions of the Bryoflora

Twelve regions have greater than 35% of the total Gulf of St. Lawrence moss flora (Table 3-14). The highest moss diversities are in western Newfoundland (FNW) and Gaspé (GAS), each having greater than 57% of the Gulf moss flora. Diversities less than 35% are found in five regions, and the lowest are on the Gulf islands of Magdalen (MDI) and Anticosti (ANT) (24% and 18% of the total Gulf flora respectively).

In comparison to the mosses, the hepatics show very different diversity patterns (Table 3-14). Only eight of the 17 regions have diversities greater than 35% of the total hepatic flora, and the remaining nine regions have diversities substantially lower than 35%.

If one expects the hepatics to have regional diversities in equal proportions to the mosses, then many regions are floristically poor in hepatics. This likely reflects a lack of records of hepatics in many Gulf regions. For this reason, in this study, less emphasis is put on hepatic Gulf of St. Lawrence distributions with respect to their migrational and dispersal histories in the region.

In eleven regions, the disjunct mosses comprise 20 to 30% of the total regional moss flora. Four regions, Northern Peninsula (FNW), southwest Newfoundland (FSW), Gaspé (GAS), and southern Labrador (NOE) have disjunct moss floras greater than 30% of the regional floras (Table 3-14). Disjunct mosses are a relatively unimportant component in the moss floras of the Magdalen Islands (MDI) and the Quebec North Shore (NOW).

Disjunct hepatics comprise a generally larger proportion of the regional hepatic floras (Table 3-14). Nine regions have disjunct bryophytes comprising greater than 30% of the regional flora, with the highest percentage in Gaspé (GAS). Northern New Brunswick (NBN) has an equally high proportion of disjuncts (46%), but this region has a known hepatic flora of only 13 species. Only six regions have percentages of disjuncts between 20% and 30%, and two regions, Magdalen Islands (MDI) and Prince Edward Island (PEI) have less than 20% of their hepatic floras represented by disjuncts.

The results of the analyses of the frequencies and diversities of the disjunct species (Tables 3-8 to 3-15, Figures 3-2 to 3-13) show that each migrational/dispersal group recognized includes species showing generally similar Gulf of St. Lawrence distributions.

Two patterns can be seen with respect to each of frequency and diversity. Frequency distributions of the migrational/dispersal groups show groups to

contain either species that are very rare to occasional within the Gulf, or species that are occasional to very common in the region. As will be shown below, only one group, the migrants from the south, shows the latter pattern.

Diversity patterns include migrational/dispersal groups which have either a northern bias within the study area, or which show a gradual decline in diversity northwards through the study area. Only one group shows this latter pattern (migrants from the south). Groups with a northern bias show generally show high diversities in the northern regions of the study area, and in particular, Gaspé and the Newfoundland Northern Peninsula. Low diversities are evident in the Maritime Provinces.

Several breaks, or abrupt changes in diversity, are evident in the migrational/dispersal groups which show a northern bias within the Gulf (all except migrants from the south). Major breaks occur between southern Labrador (NOE) and the Northern Peninsula (FNW) at the Strait of Belle Isle, and also between northern New Brunswick (NBN) and Gaspé (GAS). In some groups, minor breaks are evident between the Northern Peninsula and southwest Newfoundland as well as between Cape Breton (NSN) and central Nova Scotia.

The frequencies (Table 3-8) of migrants from the south indicate that about 80% of species in this migrational/dispersal group are occasional to very common in the Gulf. Also, the regional diversity of the mosses shows a general decrease

northward through the study area (Figure 3-2). Southern Nova Scotia (NSS) has the highest proportion of its moss flora represented by southern migrants (75%), and the proportion decreases northward to about 25% in southern Labrador (NOE). The decline is well illustrated along the eastern seaboard of Nova Scotia, western Newfoundland and southern Labrador (Figure 3-2). This pattern is much less evident among the hepatics (Figure 3-3) which show highest diversities in southwestern Newfoundland (FSW), Cape Breton Island (NSN), south coast Newfoundland (FS), and Gaspé (GAS) and the lowest diversities in New Brunswick, the North Shore (NOW), and Southern Labrador (NOE). These results probably reflect unequal collecting data for hepatics.

Bryophytes which migrated from the north are mostly rare to occasional in the study area, and these frequency classes include 77% of the species in the group (Table 3-9). The highest diversities (Figures 3-4, and 3-5) are in regions in the northern part of the study area. Regional diversities of both the mosses and the hepatics are highest in Gaspé (GAS) and on the Northern Peninsula (FNW). All 26 species in this migrational/dispersal group are found in this latter region and 19 of them are known from Gaspe. This result is unexpected, since species which migrated from the north should show a gradual decline in diversity from north to south through the study area (analogous to the pattern shown by the migrants from the south). The highest diversities might have been expected in southern Labrador (NOE) and the Quebec North Shore (NOW) where most of the migrants from the north would have been expected to reach their southern limits.

The remaining migrational/dispersal groups show rather similar frequencies and diversity patterns within the Gulf of St. Lawrence. Eighty-two percent of bryophytes supporting migration from the north and/or west (Tables 3-10) are rare to occasional in the study area, while species supporting survival in refugia (Table 3-13) and survival in refugia and/or introduction by man (Table 3-12) are very rare to rare within the study area.

Bryophytes supporting survival in refugia and/or migration from the west are also mostly very rare to rare (Table 3-10). These frequency classes comprise 78% of the species in the group. The overall frequency distribution is very similar to the refugial history group (Table 3-13).

The migrational/dispersal groups discussed above (except for migrants from the south) show the highest diversities in regions of the Gulf supporting tundra vegetation, although not all regions with tundra have high diversities. The highest diversities occur in western Newfoundland (FSW, FNW) and Gaspé (GAS). Southern Labrador (NOE) and the North Shore (NOW), however, show low diversities despite the presence there of extensive coastal tundra.

Each migrational/dispersal group, with examples of actual Gulf distributions, is discussed below.

Migration from the South. The patterns of diversity (Figure 3-2, and 3-3)

indicate that the Gulf distributions of migrants from the south show a gradation from species which are widespread throughout the Gulf (e.g., *Bazzania trilobata* Figure 4-1), to species restricted to its southern portions (Figures 4-1 to 4-4).

Several species do not follow these patterns. *Grimmia donniana* is mainly restricted to the barren mountains and highlands of western Newfoundland and Gaspé, whereas *Rhytidium rugosum* is primarily a coastal species and *Seligeria donniana* shows, surprisingly, a northern bias in the study area.

Migrants from the North. Many (69%) of the bryophytes which may have migrated to the Gulf from the North have a northern distribution in the study area and are absent from the Maritimes (NBC, NBN, NBS, NSC, NSN, NSS). Of these, several are widespread in regions with tundra vegetation, e.g., *Dicranum elongatum*, *Gymnomitrium concinnatum*, but most have rather restricted distributions and seven are restricted to Gaspé and western Newfoundland (*Andreaea blyttii*, *Gymnomitrium corallioides*, *Kiaeria falcata*, *Pleuroclada albescens* (Figure 4-5), *Pohlia obtusifolia*, *Polytrichastrum sexangulare* (Figure 4-6), and *Tritomaria polita*).

Only eight of the species are found in the Maritimes and seven are rare in this region but more common in the northern portion of the study area, e.g., *Brachythecium turgidum*, *Desmatodon latifolius*, *Distichium inclinatum*, *Kiaeria blyttii*, *K. starkei*, *Plagiobryum zierii* (Figure 4-7), *Pohlia drummondii* (Figure 4-8).

Figure 4-1. The distribution of *Bazzania trilobata* in the Gulf of St. Lawrence (open circles are literature reports from Schuster (1969)).

Figure 4-2. The distribution of *Pylaisiella intricata* in the Gulf of St. Lawrence (circles with triangles are county records from Ireland (1982)).

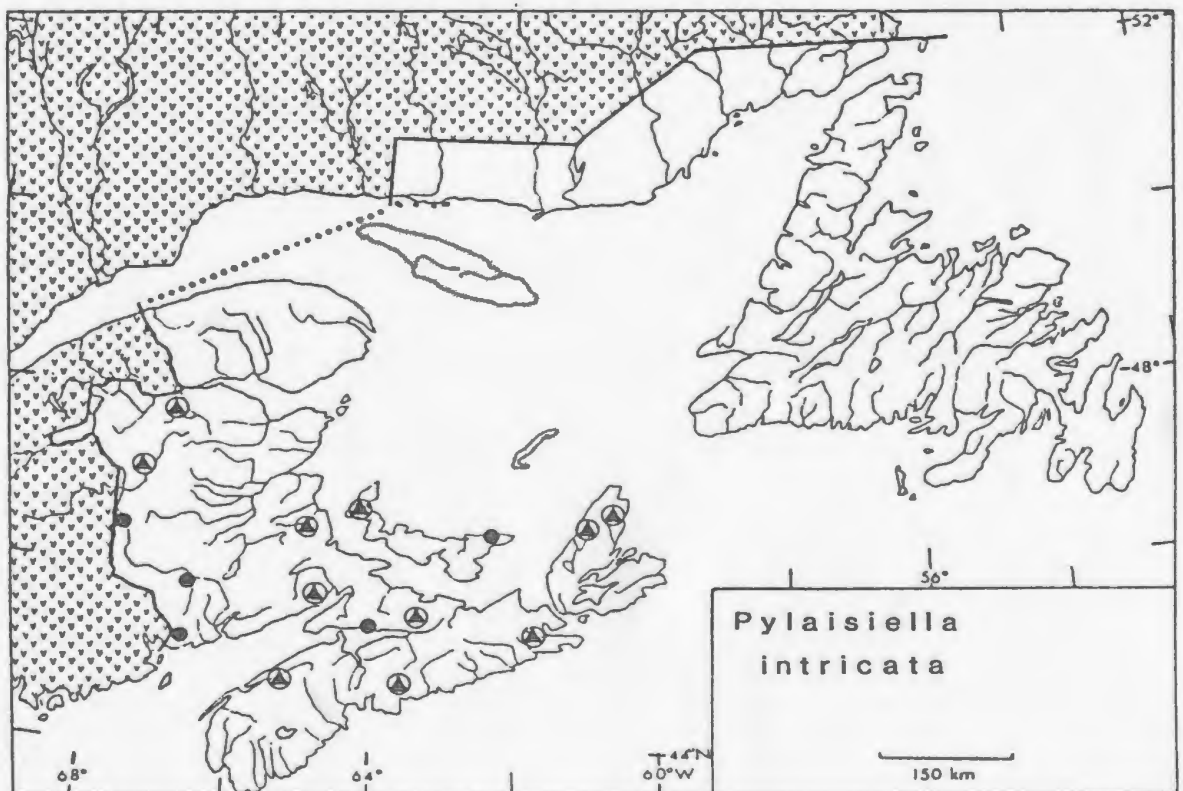
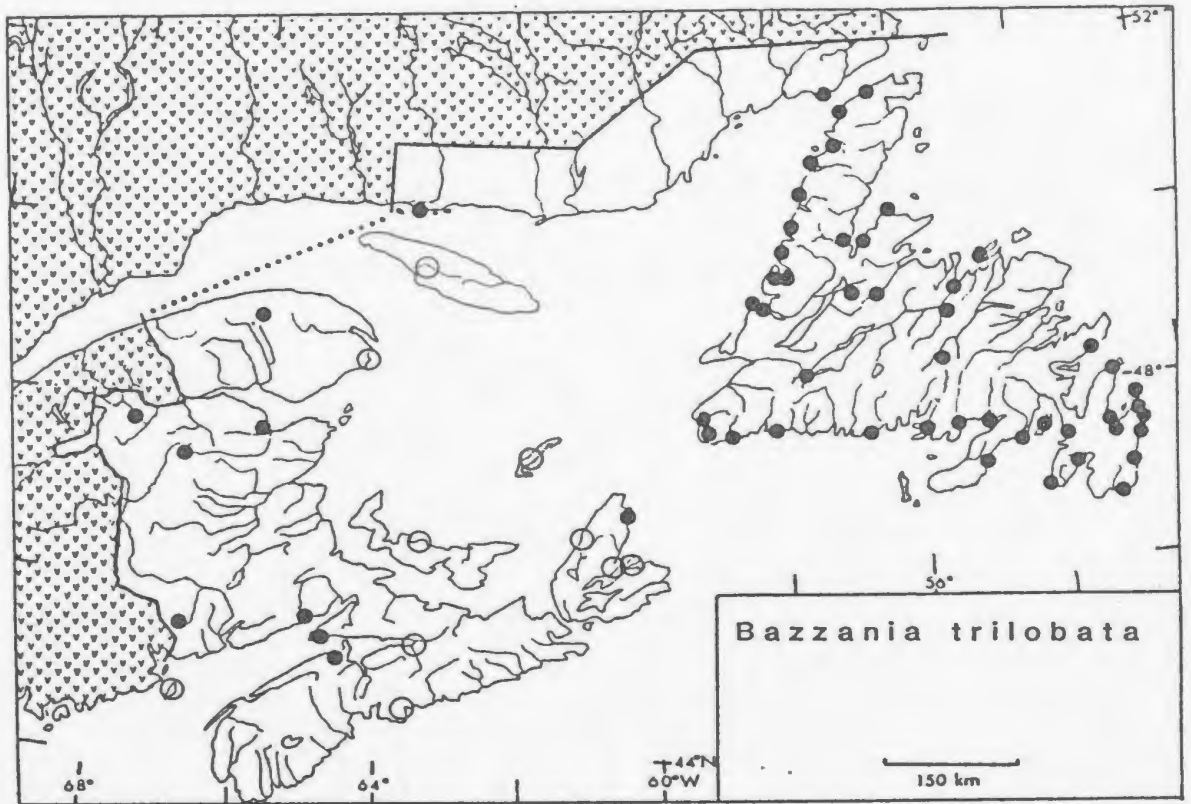


Figure 4-3. The distribution of *Dichelyma capillaceum* in the Gulf of St. Lawrence (circles with triangles are county records from Ireland (1982)).

Figure 4-4. The distribution of *Isopterygium distichaceum* (circles with triangles are county records from Ireland (1982)).

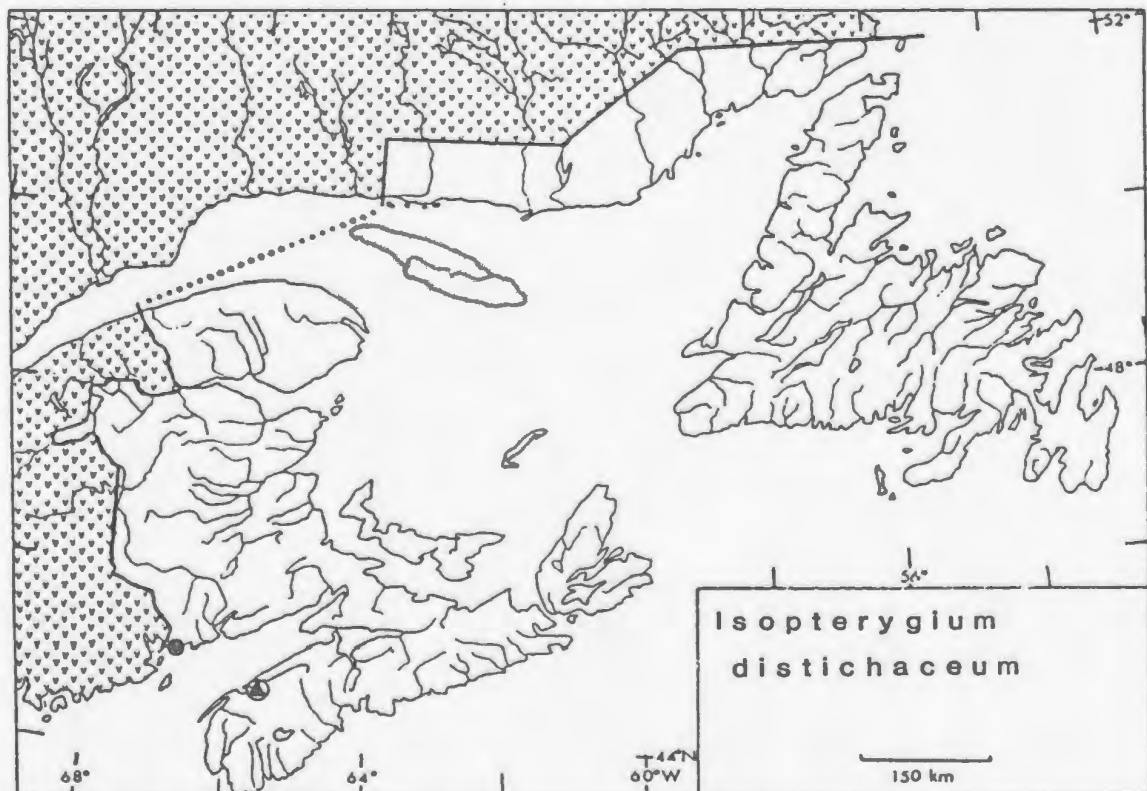
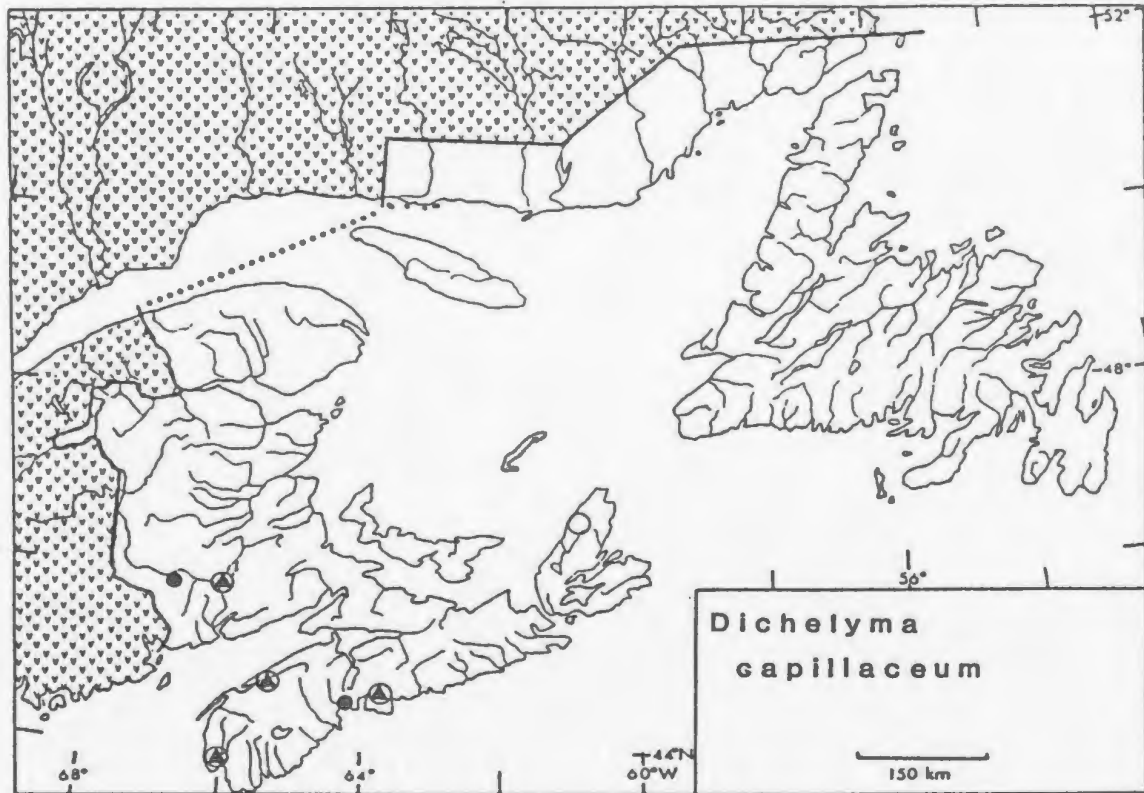
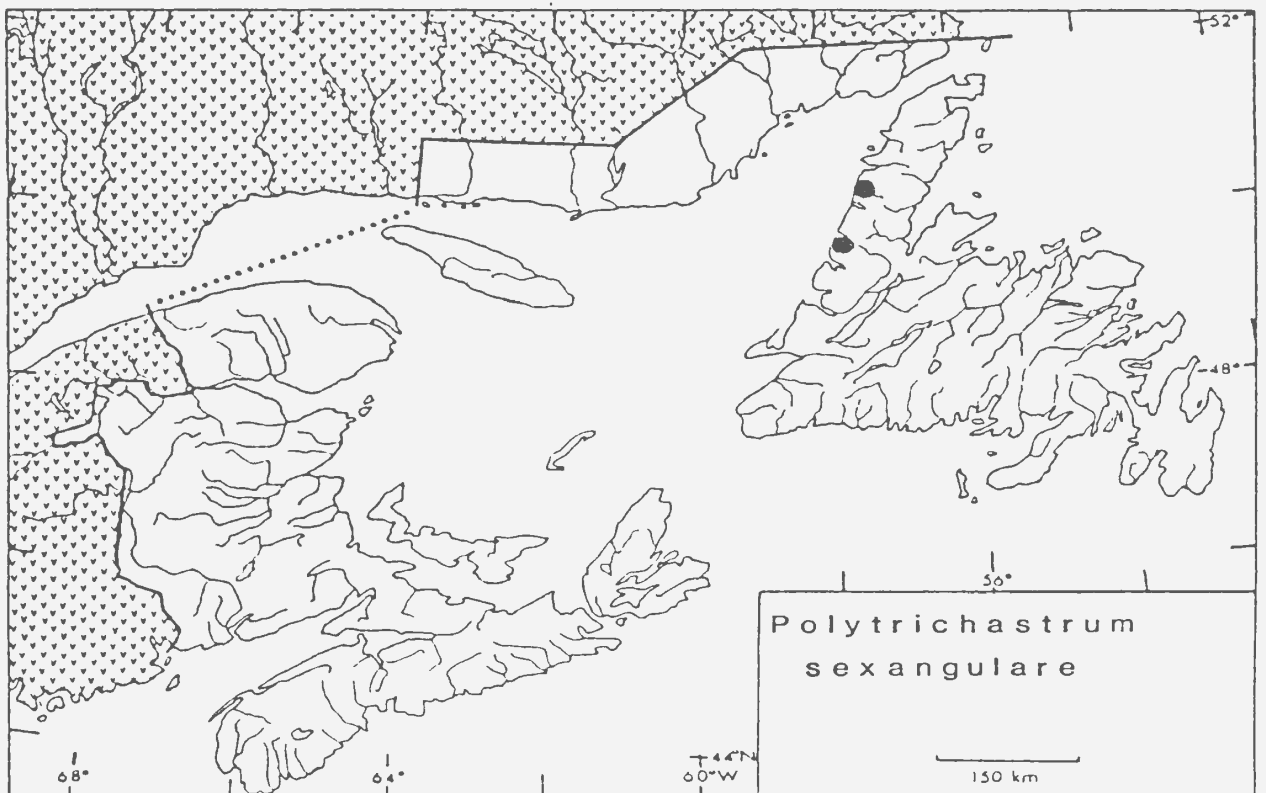
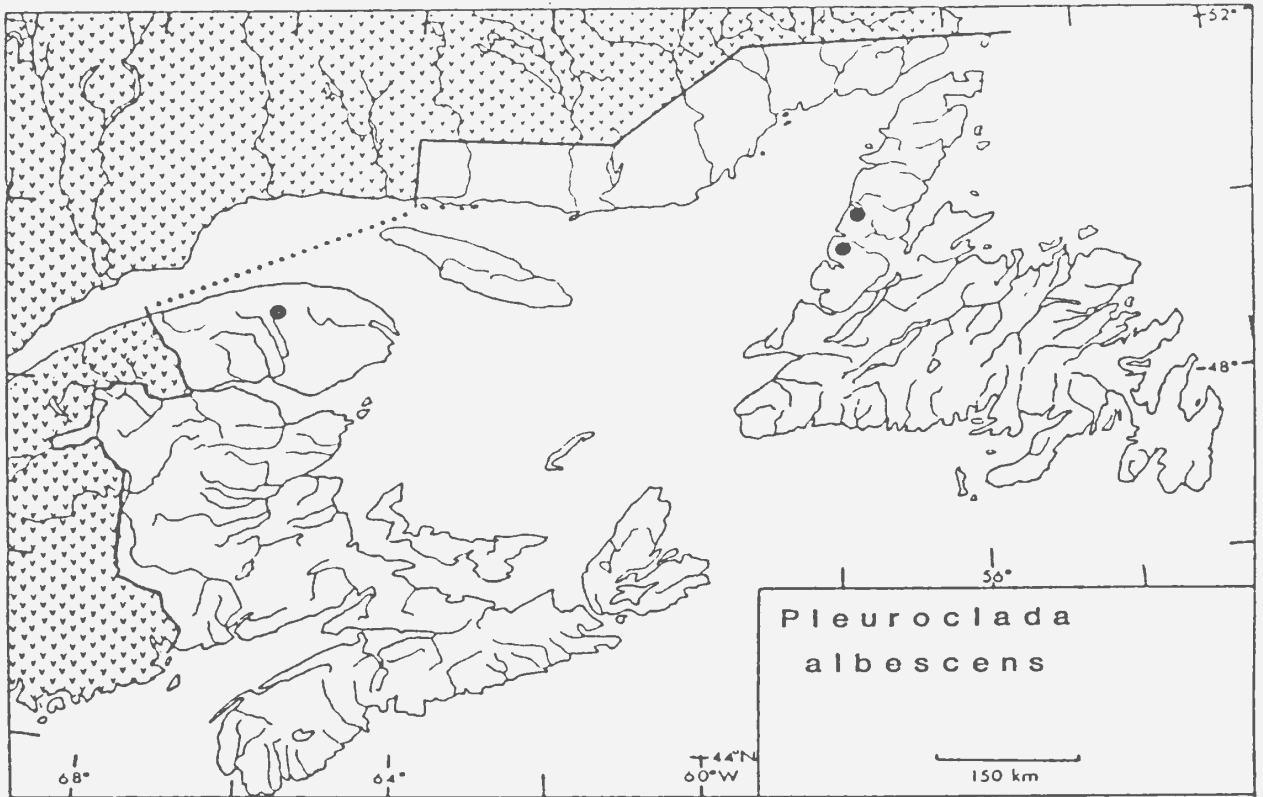


Figure 4-5. The distribution of *Pleuroclada albescens* in the Gulf of St. Lawrence.

Figure 4-6. The distribution of *Polytrichastrum sexangulare* in the Gulf of St. Lawrence.



The coastal moss *Schistidium maritimum* is the only species in this migrational/dispersal group which is widespread in the study area.

Migrants from the North and/or West. As with the preceding group, the majority of species are found in the northern regions of the study area, and are generally absent in the Maritimes. Nine species (56%) have this northern bias. Most are known from three to four regions (although rare), e.g., *Anthelia juratzkana*, *Aulacomnium turgidum* (Figure 4-9), *Chandonanthus setiformis* (Figure 4-10), *Grimmia torquata*, *Hygrohypnum alpestre*, but two species have very restricted distributions and are known only from the high mountains of Gaspé (*Anastrophyllum saxicola*, *Myurella tenerrima*).

The remaining seven bryophytes are present in the Maritimes. Of these, five are rare and known mainly from the northern Maritimes (NBN, NSN), e.g., *Bartramia ithyphylla* (Figure 4-11), *Catoscopium nigrum*, *Barbilophozia lycopodioides*, *Timmia austriaca* (Figure 4-12), *Odontoschisma macounii*.

Only two species supporting this history are found throughout most of the study area: *Dicranum majus*, and *Barbilophozia hatcheri*.

Migrants from the West and/or Survivors in Refugia. Many (65%) species belonging to the refugia and/or west migrational/dispersal group have a northern distribution in the study area and are absent from the Maritimes. Half (10

Figure 4-7. The distribution of *Plagiobryum zierii* in the Gulf of St. Lawrence.

Figure 4-8. The distribution of *Pohlia drummondii* in the Gulf of St. Lawrence (circle with triangle is county record in Ireland (1982); open circle, literature report from Tuomikoski *et al.* (1973)).

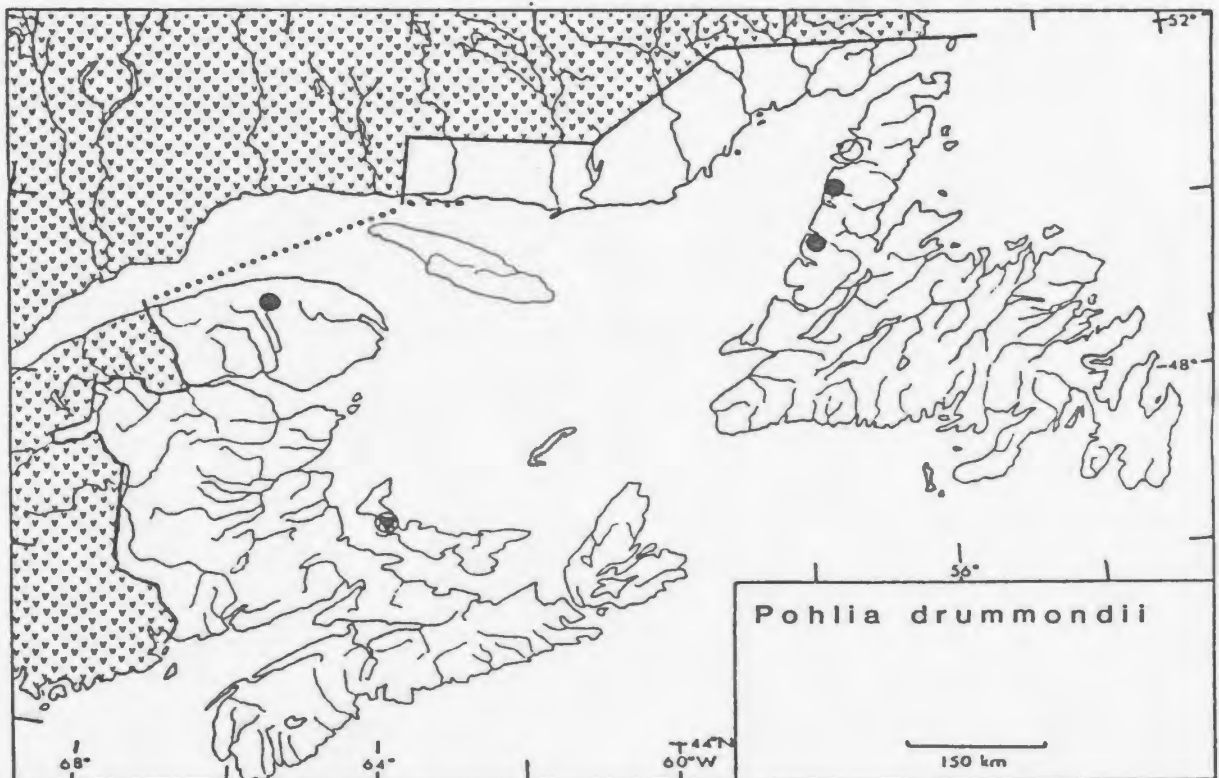
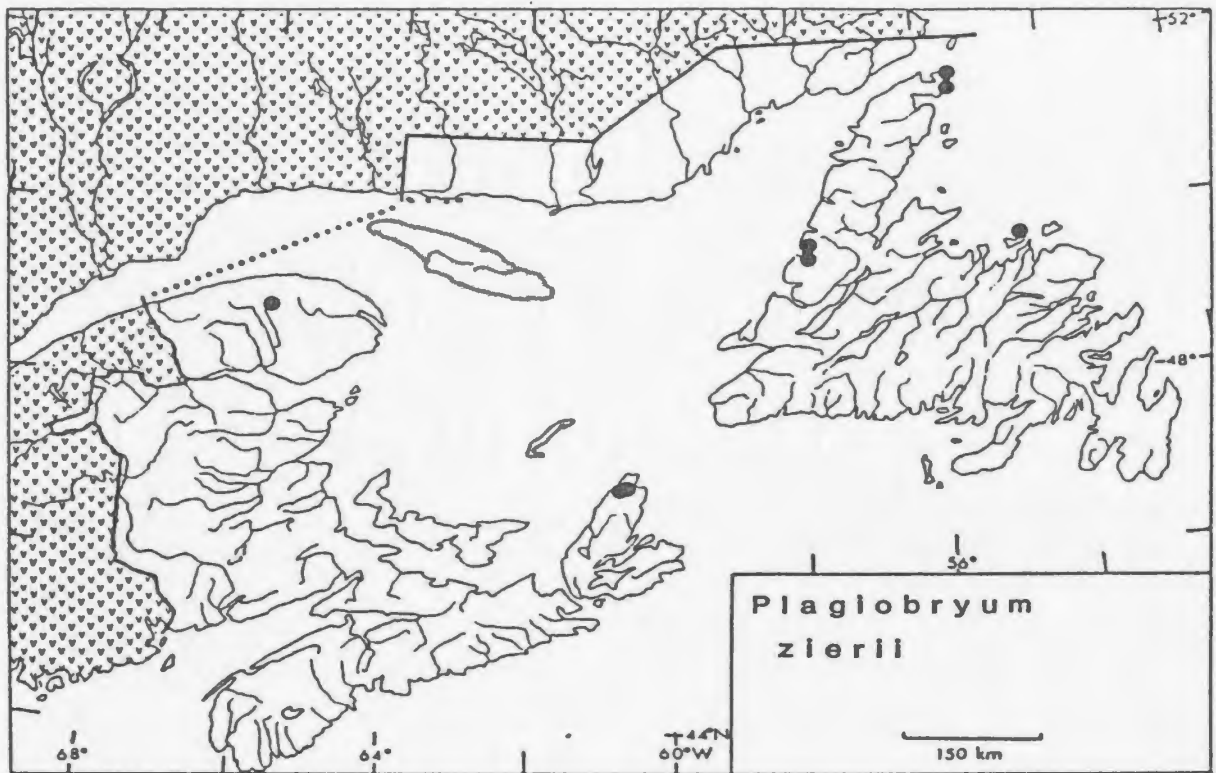


Figure 4-9. The distribution of *Aulacomnium turgidum* in the Gulf of St. Lawrence (open circle, literature report from Miller (1980a)).

Figure 4-10. The distribution of *Chandonanthus setiformis* in the Gulf of St. Lawrence (open circles, literature reports in Buch and Tuomikoski (1955)).

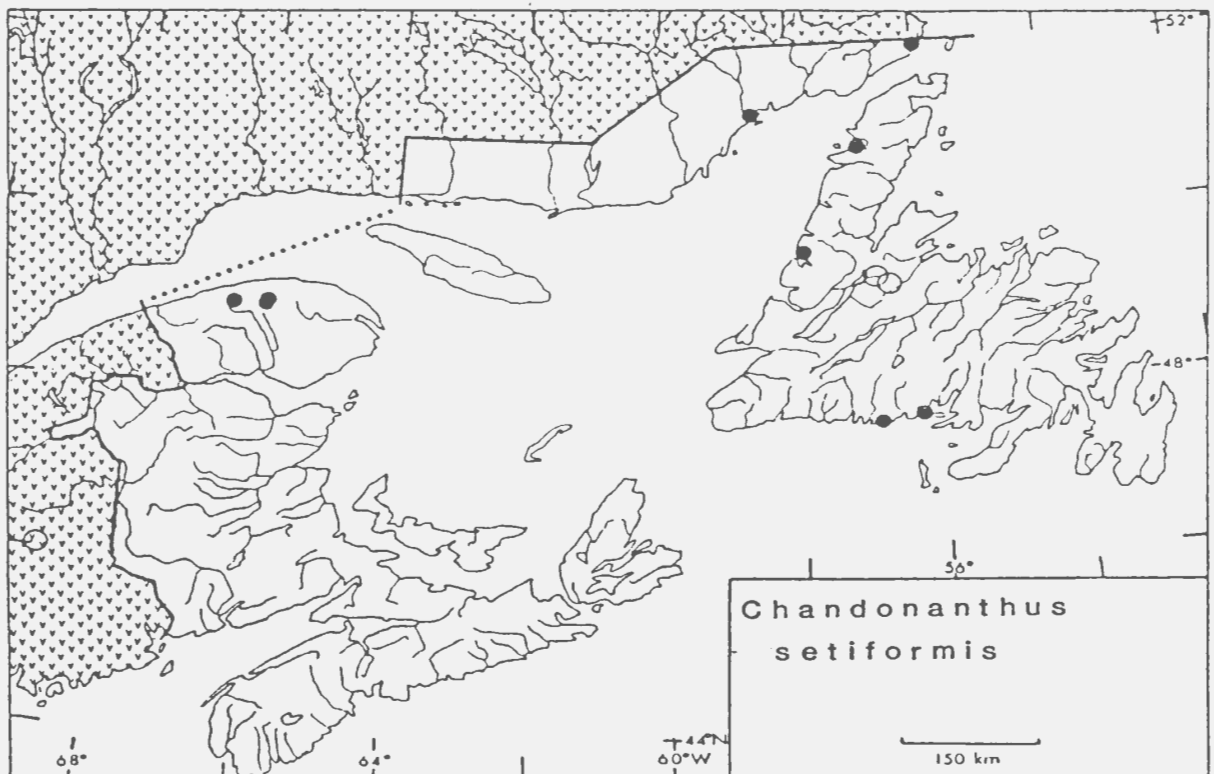
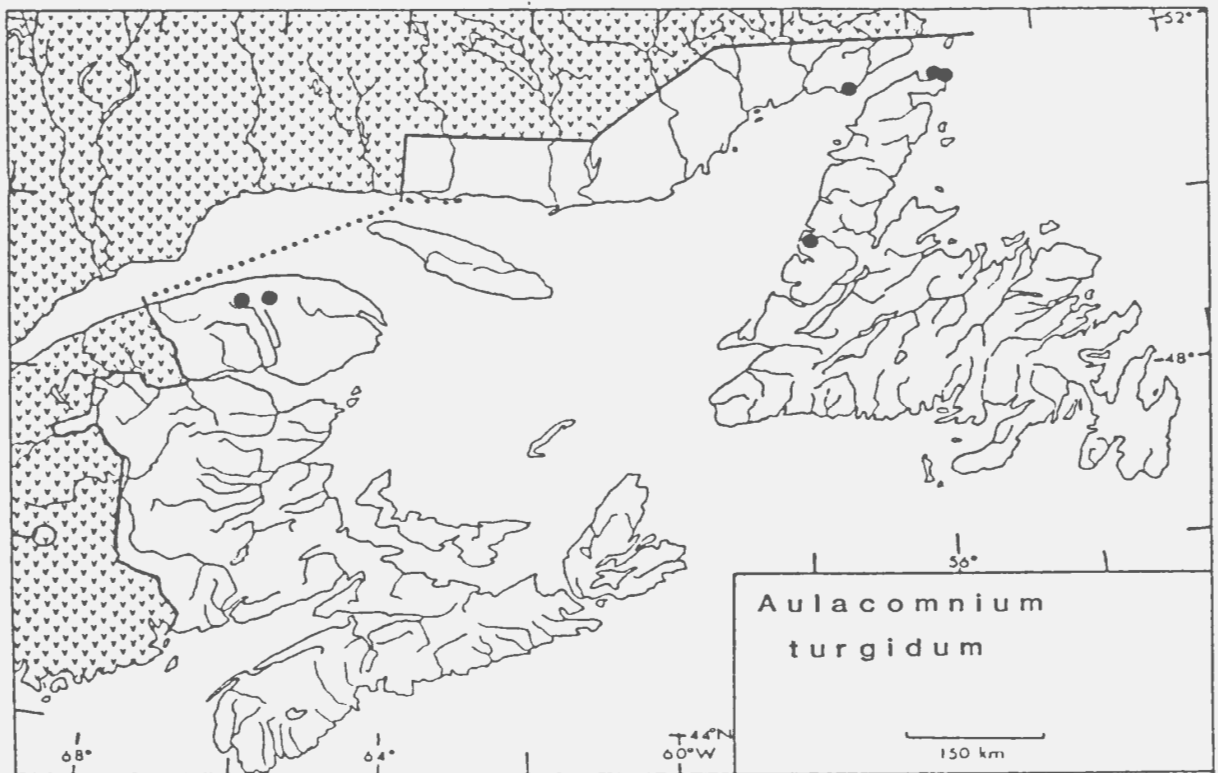
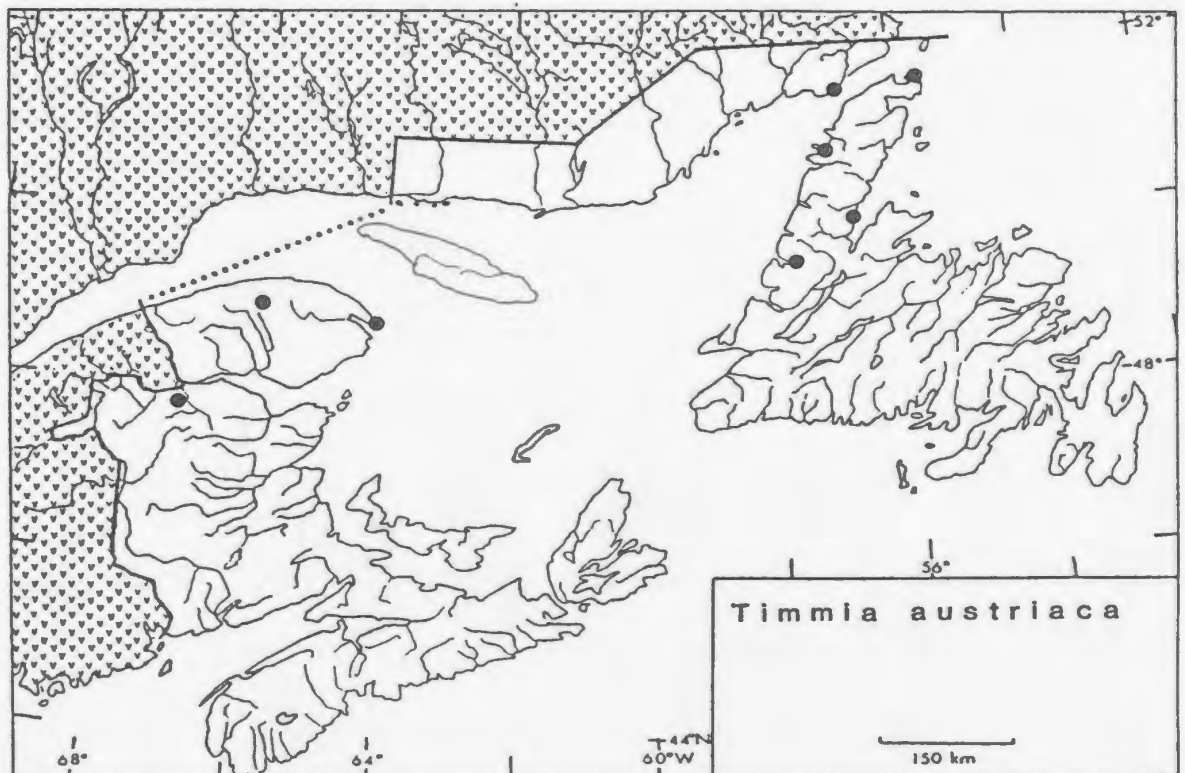
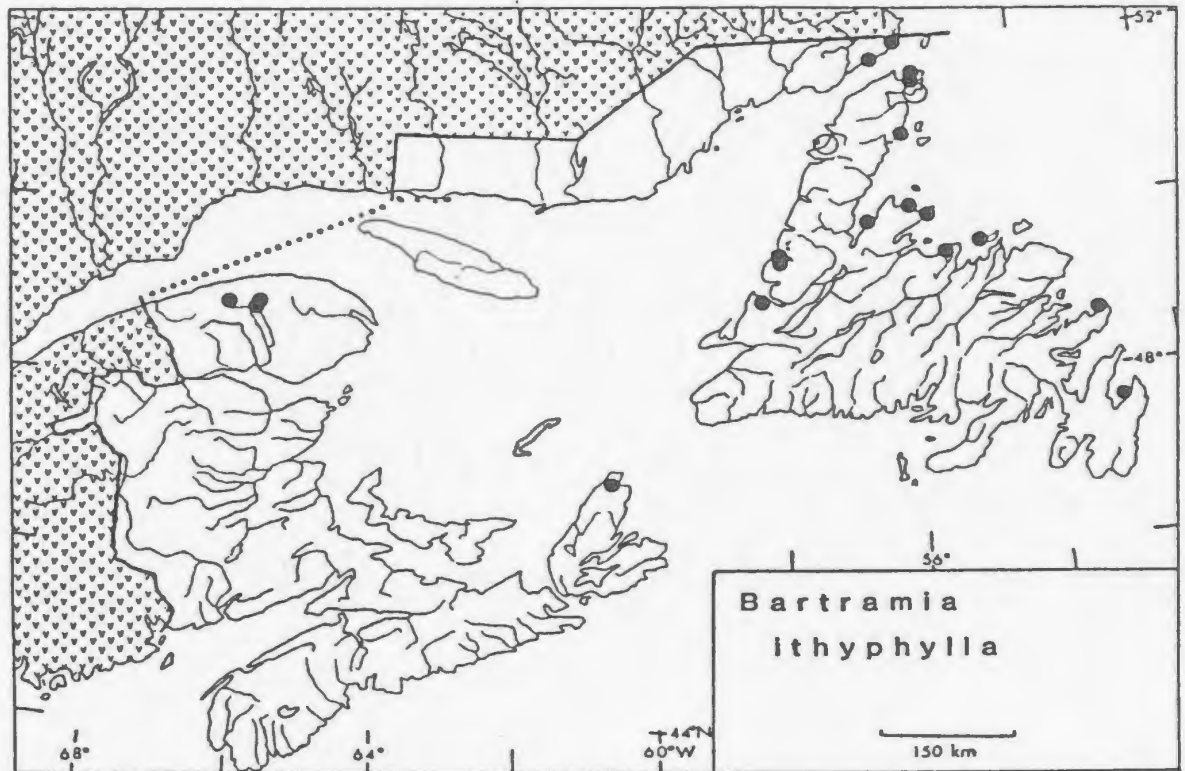


Figure 4-11. The distribution of *Bartramia ithyphylla* in the Gulf of St. Lawrence (open circles, literature reports from Tuomikoski *et al.* (1973)).

Figure 4-12. The distribution of *Timmia austriaca* in the Gulf of St. Lawrence.



species) are known only from the Gaspé Peninsula or western Newfoundland (FSW, FNW), e.g., *Clevea hyalina*, *Gyroweisia tenuis*, *Lophozia heterocolpa* (Figure 4-13), *Scorpidium turgescens*, *Tritomaria scitula*. An equal number are not restricted to these regions, e.g., *Amblyodon dealbatus* (Figure 4-14), *Lophozia wenzelii*, *Miehlichhoferia miehlichhoferi*, *Orthotrichum pallens*.

Only 11 species in this group are present in the Maritimes with five known only from Cape Breton Island (NBN), e.g., *Cephalozia loitlesbergeri*, *Marsupella sparsifolia*, *Odontoschisma elongatum*, *Pseudoleskea patens* (Figure 4-15), *Scapania gymnosmostophila*. Five are found elsewhere in the Maritimes but all are rare there (*Aloina brevirostris*, *Grimmia anodon*, *Scapania cuspiduligera*, *S. subalpina*, *Trichodon cylindricus* (Figure 4-16)).

Only one bryophyte that may have migrated from the west and/or survived in refugia is widespread throughout the study area, *Dicranella subulata*.

Survivors in Refugia. A large majority (70%) of species in the refugial group are, in the Gulf of St. Lawrence, distributed primarily in the northern half of the study area, and do not occur in the Maritimes. A surprisingly high proportion of species with this northern bias (31 of 54) are present only in Gaspé Peninsula (GAS) and/or in western Newfoundland (FSW, FNW). Some have populations in two or three of these regions, e.g., *Andreaea nivalis*, *Grimmia tenerrima*, *Harpanthus flotovianus*, but others are known only from a single

Figure 4-13. The distribution of *Lophozia heterocolpos* in the Gulf of St. Lawrence (open circles, literature reports in Schuster (1969)).

Figure 4-14. The distribution of *Amblyodon dealbatus* in the Gulf of St. Lawrence (open circles, literature reports in Lepage (1946), and Grondin and Melancon (1980)).

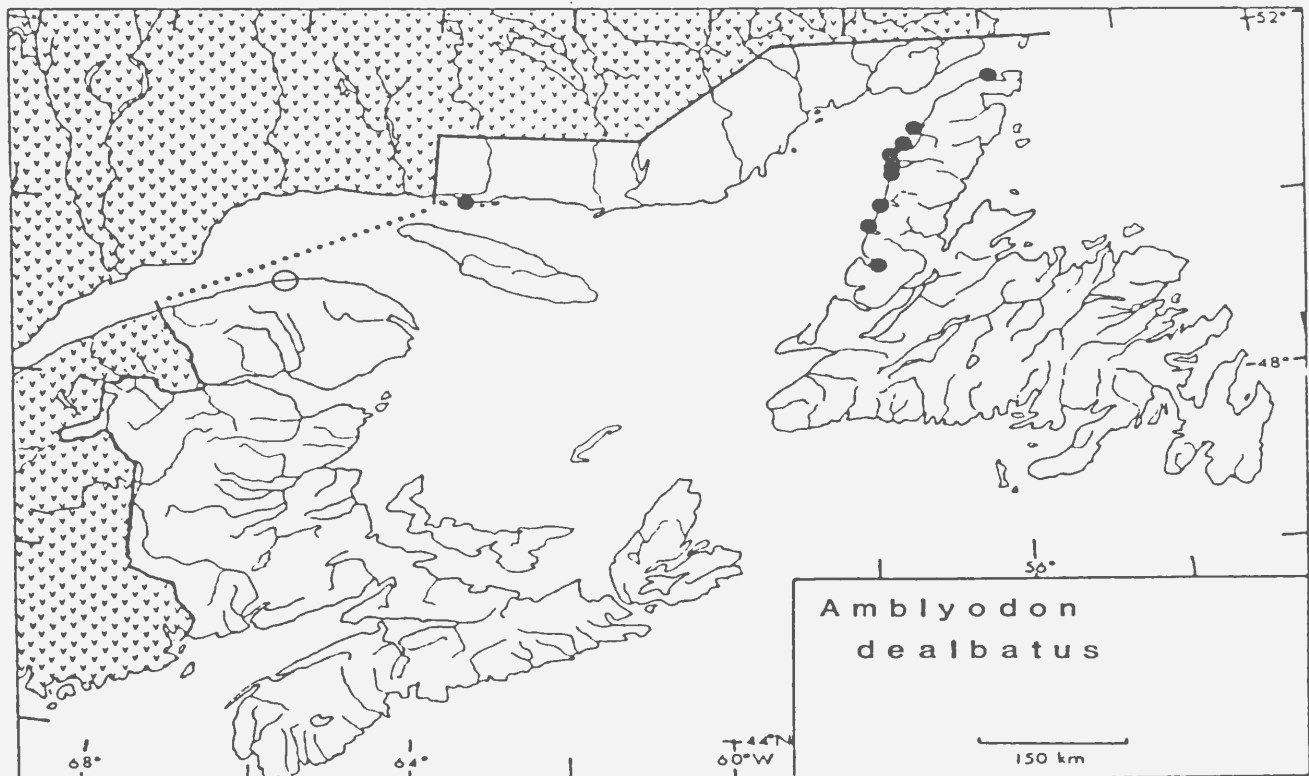
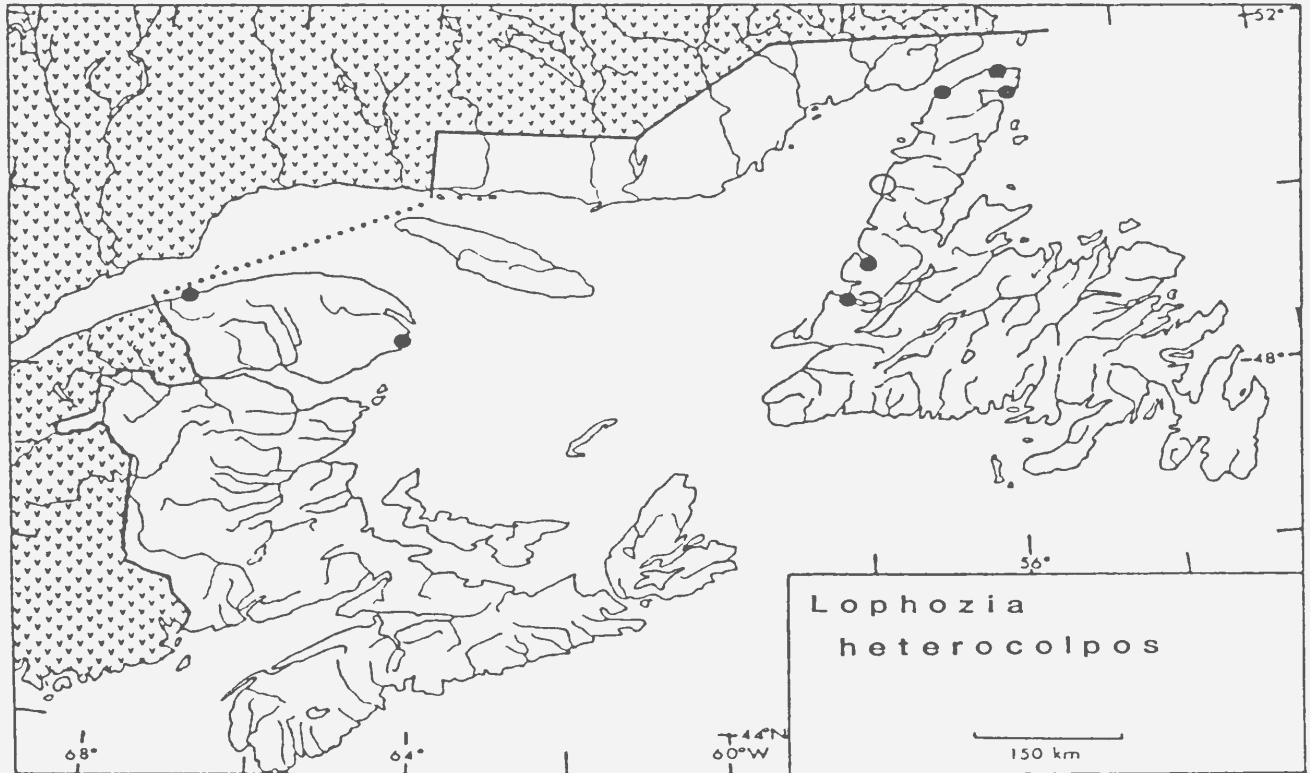
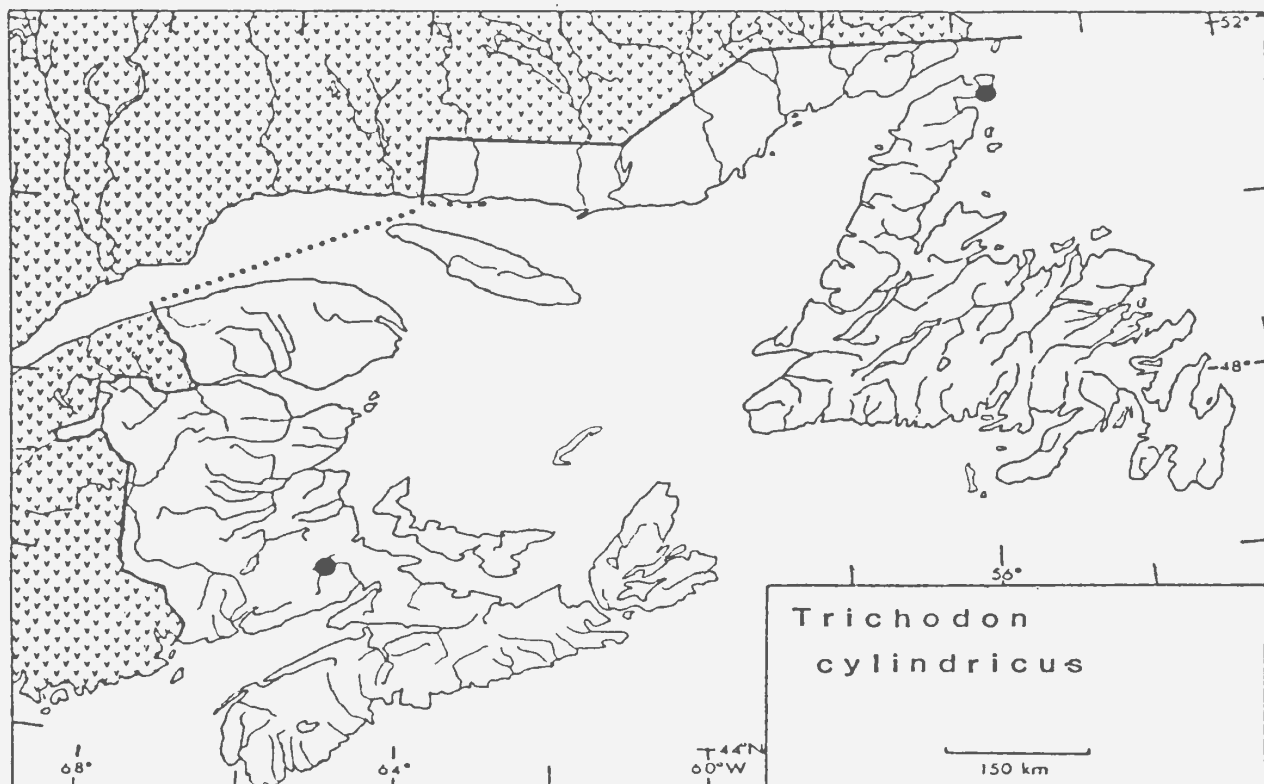
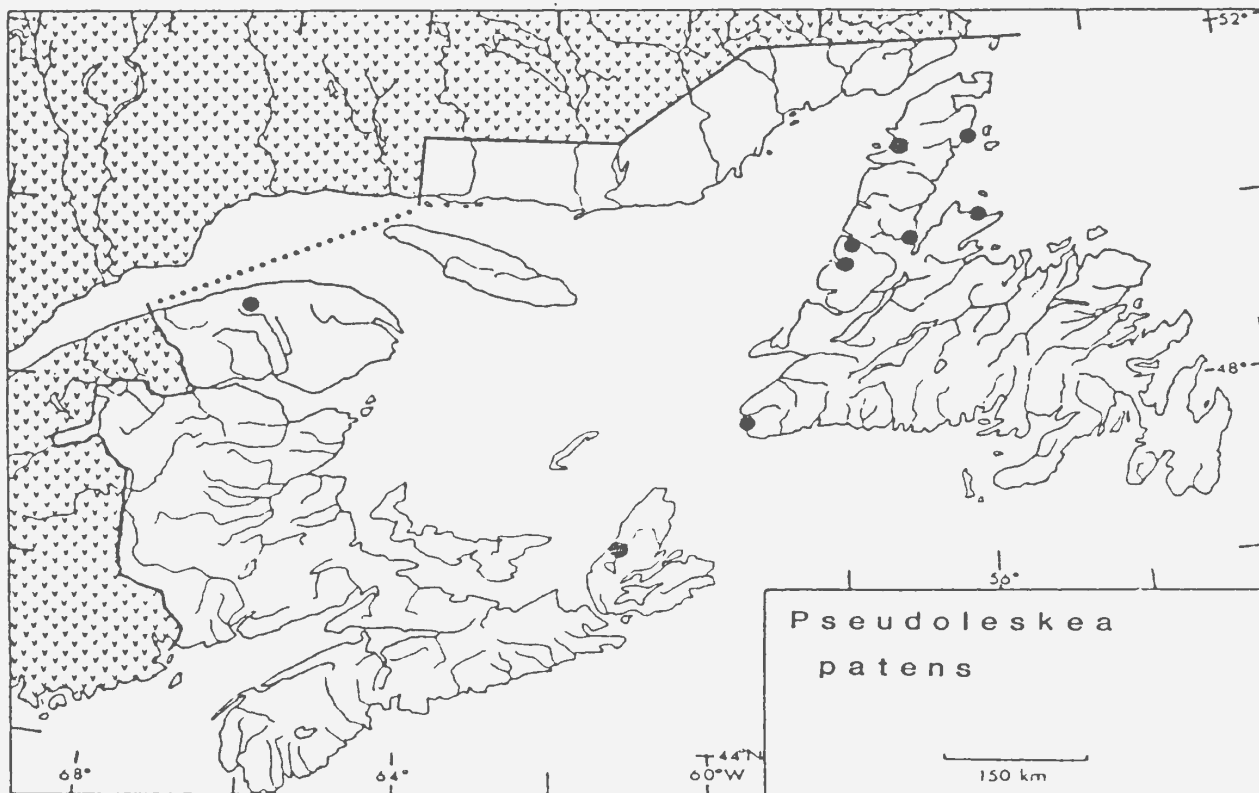


Figure 4-15. The distribution of *Pseudoleskea patens* in the Gulf of St. Lawrence.

Figure 4-16. The distribution of *Trichodon cylindricus* in the Gulf of St. Lawrence.



region, e.g., *Didymodon asperifolius*, *Hydrogrimmia mollis*, *Moerckia blyttii* (Figure 4-17). Fourteen species are known in the Gulf of St. Lawrence from one locality, e.g., *Desmatodon laureri*, *Grimmia atrata*, *Sauteria alpina*. Most of the remaining species are more widely distributed in the northern part of the study area, but are nevertheless rare, e.g., *Barbula reflexa*, *Desmatodon systilius*, *Hygrohypnum smithii*, *Lophozia bantriensis*, *Orthothecium strictum* (Figure 4-18), *Scapania paludosa*.

Twenty-four bryophytes in the refugial group are present in the Maritimes, of which 14 have primarily a northern distribution in the study area, with isolated stations in northern New Brunswick or in the Cape Breton Highlands, e.g., *Arctoa fulvella* (Figure 4-19), *Campylium halleri*, *Metacalypogeia schusterana*, *Oligotrichum hercynicum* (Figure 4-20), *Solenostoma obovatum*. The remaining ten are more or less widespread throughout the study area, e.g., *Diplophyllum albicans*, *Isothecium stoloniferum*, *Rhytidiadelphus loreus*, *Sphagnum pylaesii*, or have sporadic distributions there, e.g., *Nardia scalaris*, *Scapania umbrosa*, *S. recurvata*, *Stokesiella praelonga*, *Tayloria serrata*.

Bryophytes Which Survived Glaciation in Gulf Refugia, or Were Introduced by Man. Of all the migrational/dispersal groups, the study area distributions of this group show the most variation. Two bryophytes are widespread throughout the study area, *Tetraphis geniculata* (Figure 4-21) and

Figure 4-17. The distribution of *Moerckia blyttii* in the Gulf of St. Lawrence.

Figure 4-18. The distribution of *Orthothecium strictum* in the Gulf of St. Lawrence (open circle, literature report from Tuomikoski *et al.* (1973)).

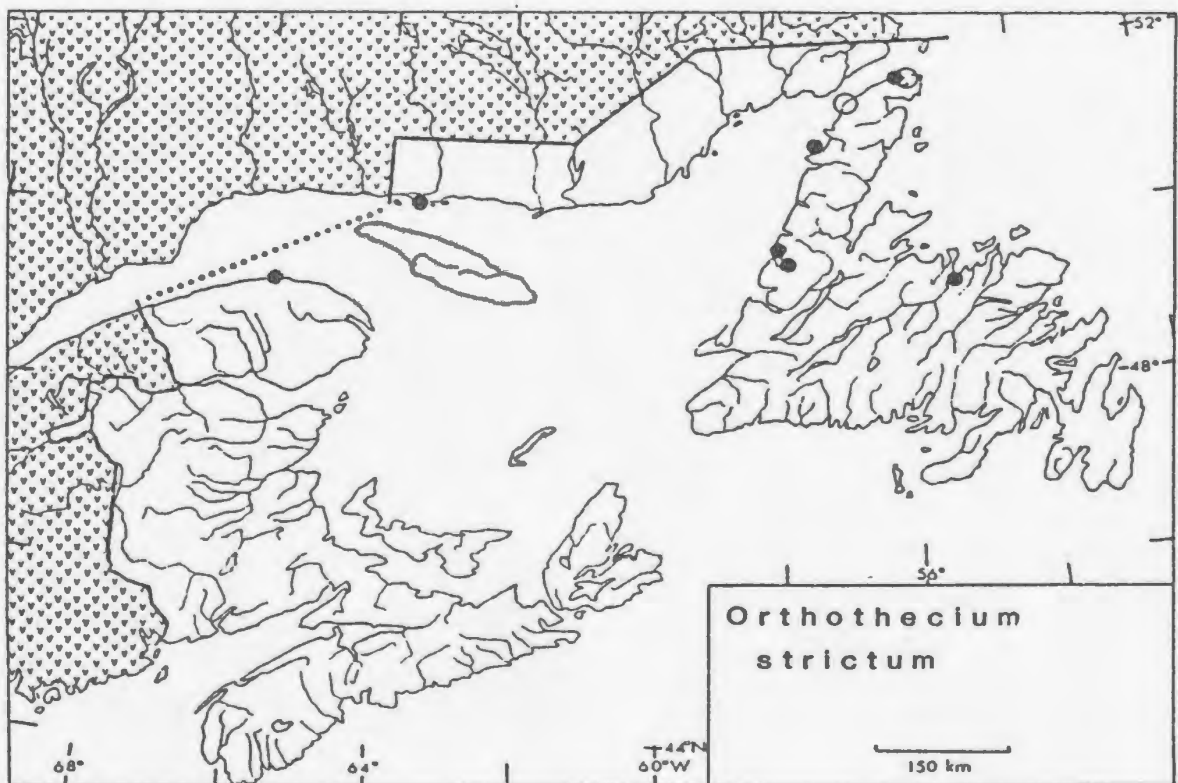
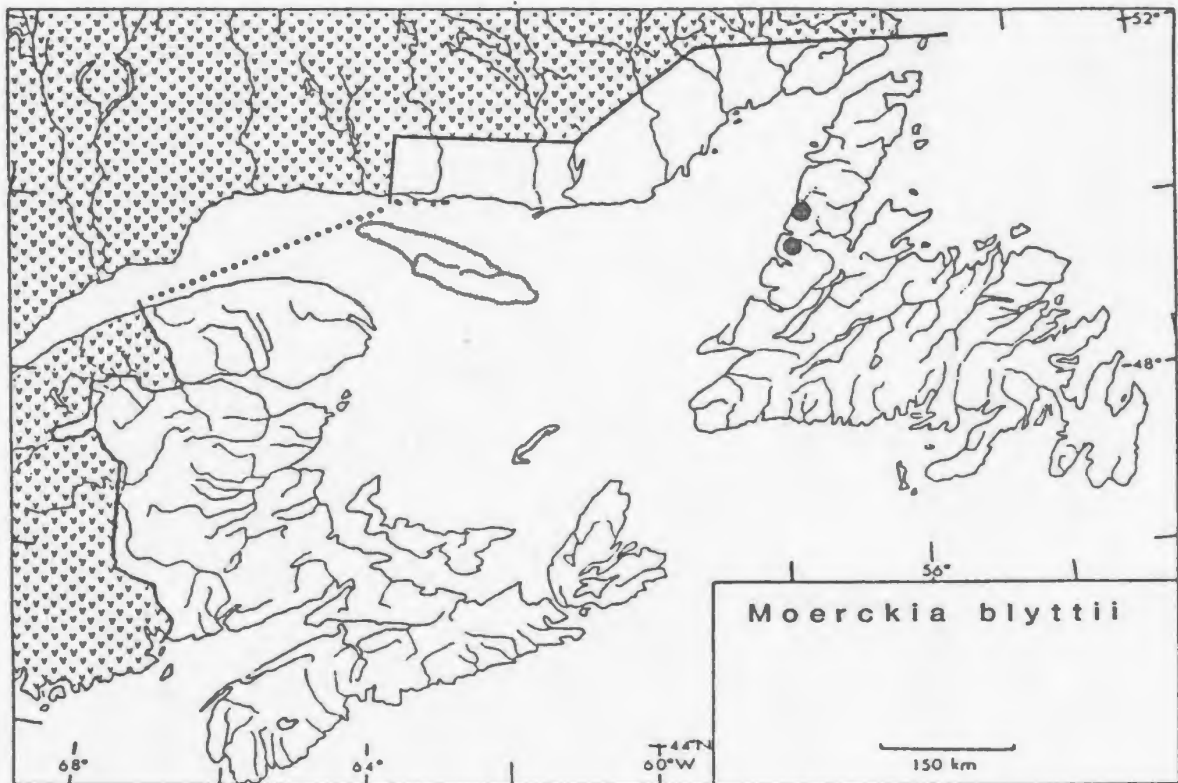
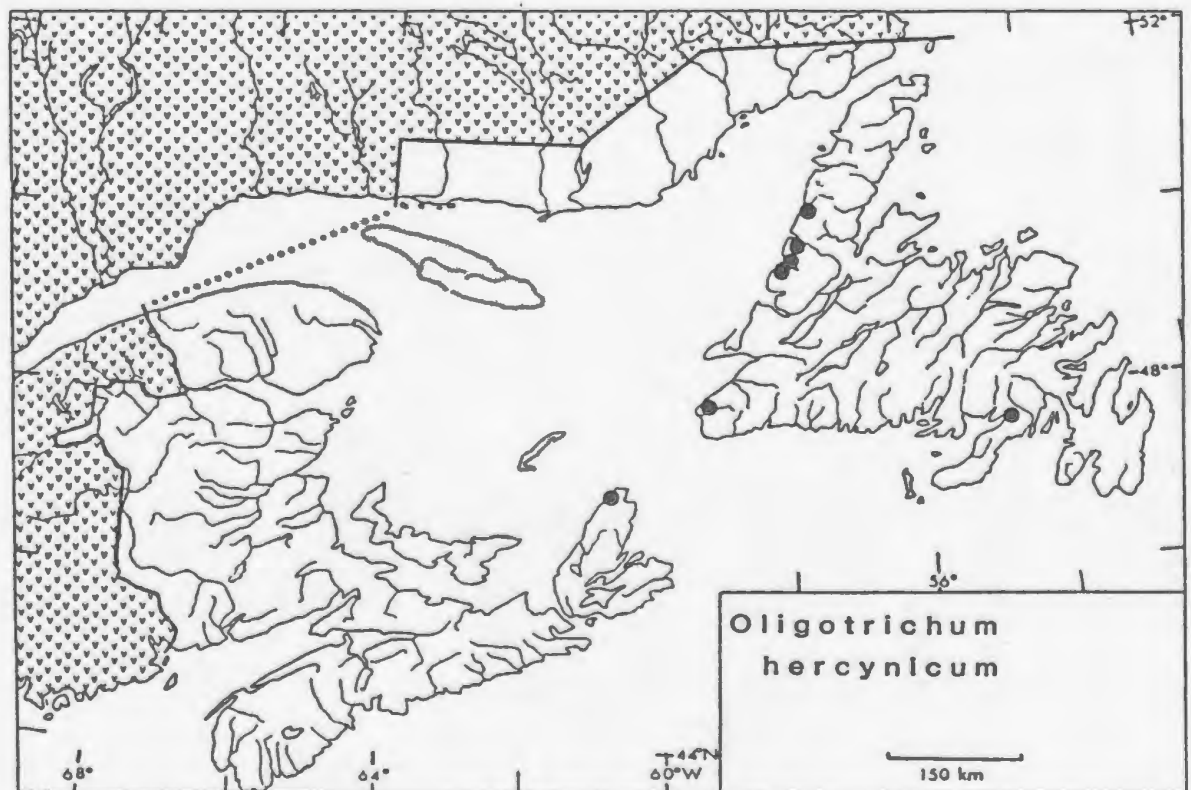
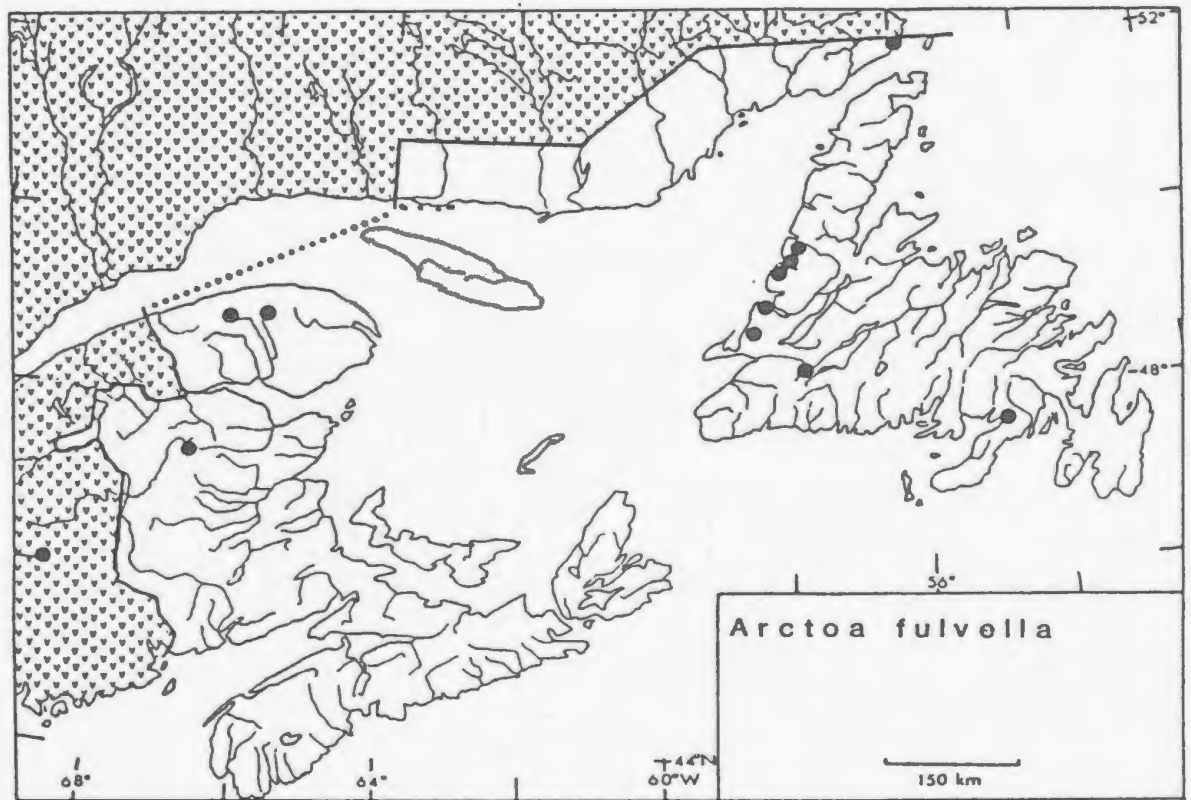


Figure 4-19. The distribution of *Arctoa fulvella* in the Gulf of St. Lawrence.

Figure 4-20. The distribution of *Oligotrichum hercynicum* in the Gulf of St. Lawrence.



Ulota phyllantha, and eight are found only in the northern portion of the study area. Seven are frequent in several regions and occur primarily in the northern portion of the study area, e.g., *Homalothecium sericeum*, *Orthotrichum gymnostomum*, *Schistidium trichodon*, *Seligeria tristichoides* (Figure 4-22). Two additional species in this group are restricted to eastern Newfoundland (*Thuidium tamarascinum*, *Pseudoscleropodium purum*). Four species are very rare and are known from only one site, e.g., *Bryum warneum* (NOW), *Cynodontium jenneri* (FE), *Trematodon montanus* (FNW) and *Orthotrichum stramineum* (FE) (Figure 4-23). Unlike the other bryophytes in this migrational/dispersal group, *Zygodon conoideus* (Figure 4-24) has a southern distribution in the Gulf. This species is known primarily from central and southern Nova Scotia but has a single station southwestern Newfoundland.

4.2. Discussion of Possible Migrational/Dispersal Histories With Reference to Eastern North American Distribution Patterns

4.2.1. Migration from the South

Postglacial migration to the Gulf of St. Lawrence from the south has been given little attention for disjunct bryophytes, although this dispersal history has been assumed to be important for the flora as a whole. This study has shown that even for disjuncts, such a migration history is important and accounts for 39% of the disjunct bryophyte flora of the Gulf. Only the "survival in refugia" history comprises a larger proportion of the disjunct bryophyte flora of the Gulf.

Figure 4-21. The distribution of *Tetraxis geniculata* in the Gulf of St. Lawrence (open circles, literature reports from Forman (1962), Grondin and Melancon (1980), and Tuomikoski *et al.* (1973); circles with triangles are county reports in Ireland (1982)).

Figure 4-22. The distribution of *Seligeria tristichoides* in the Gulf of St. Lawrence.

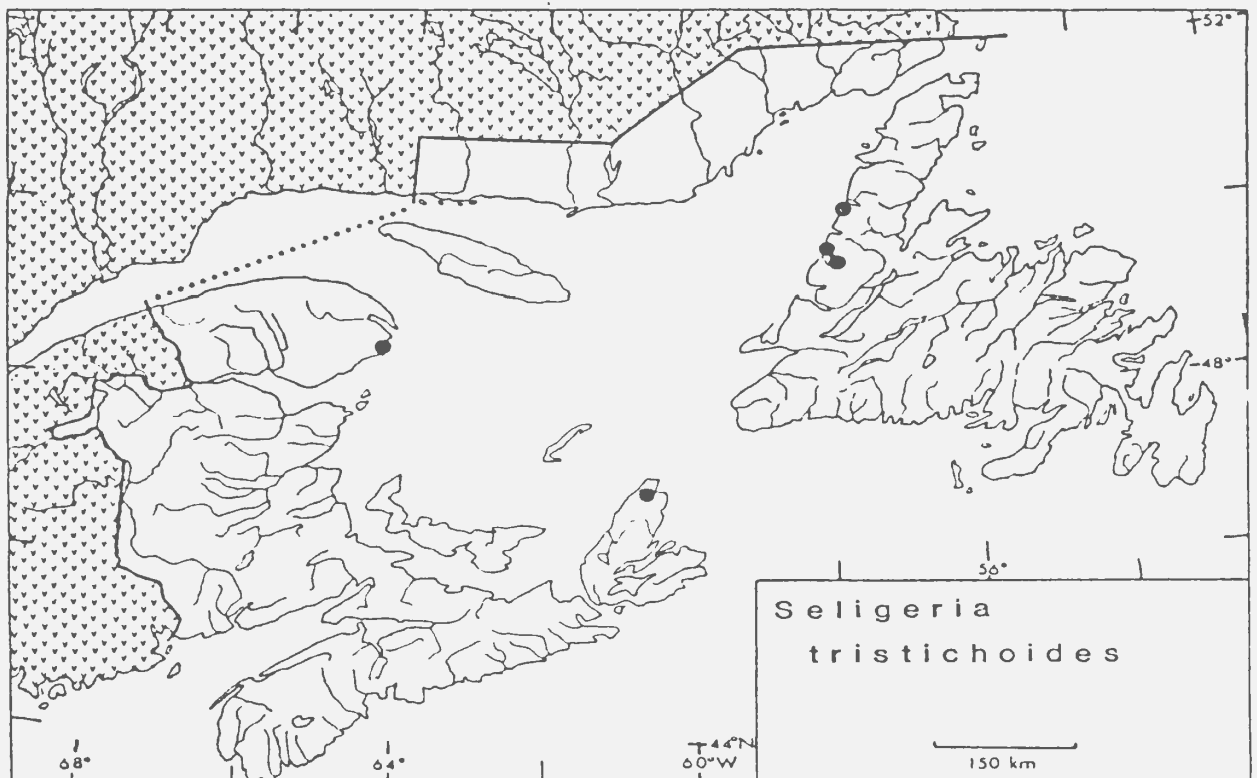
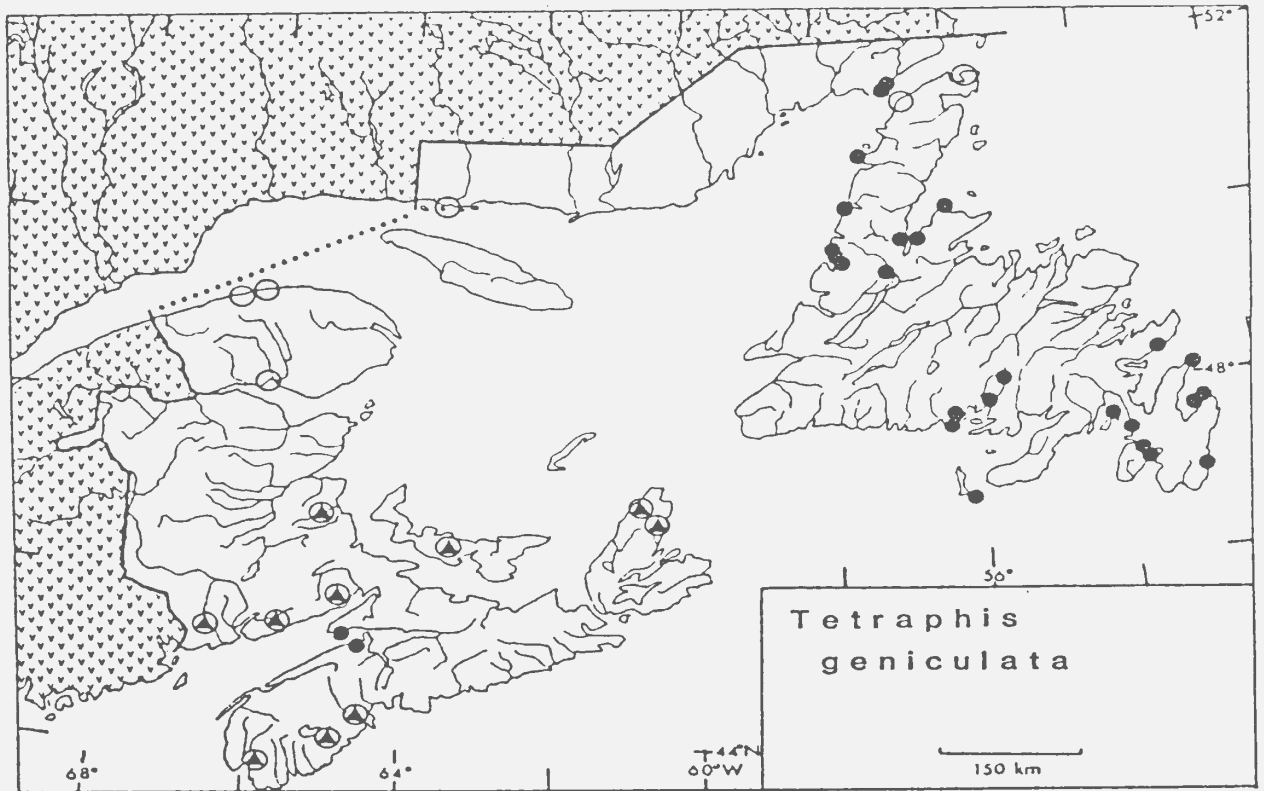
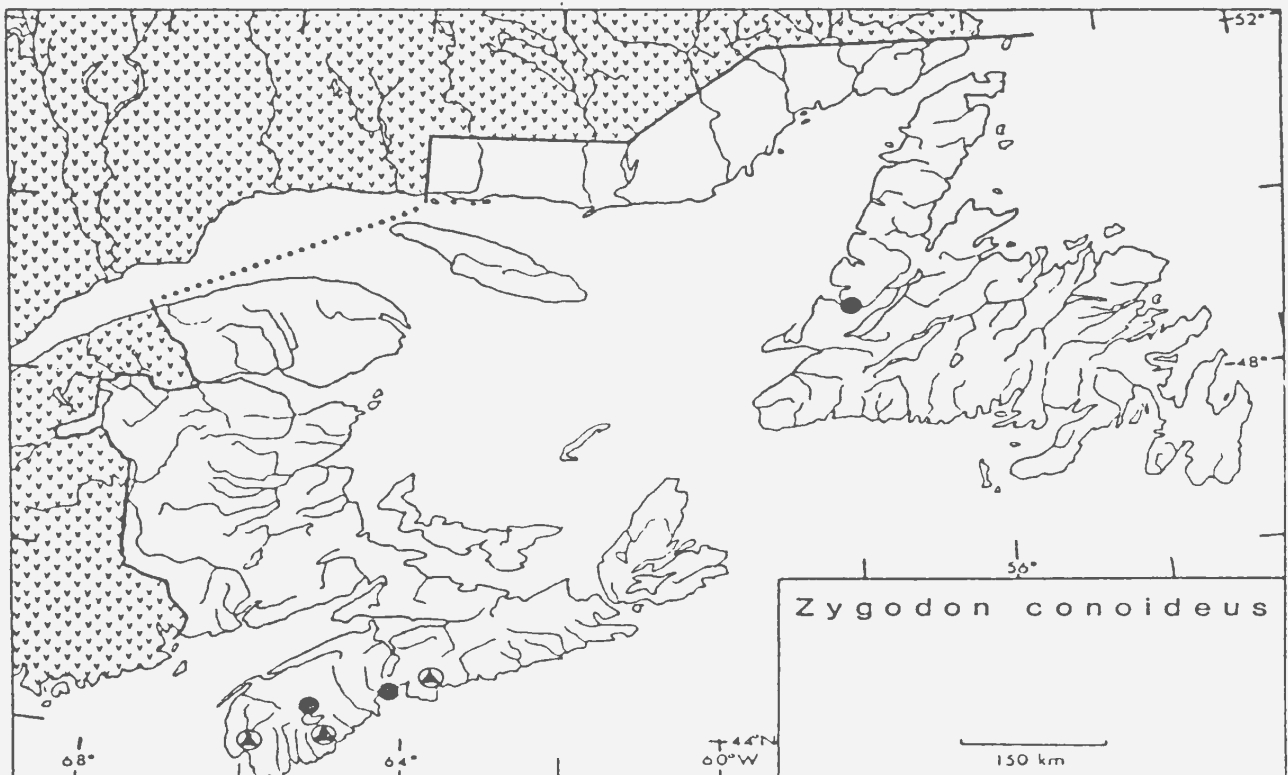
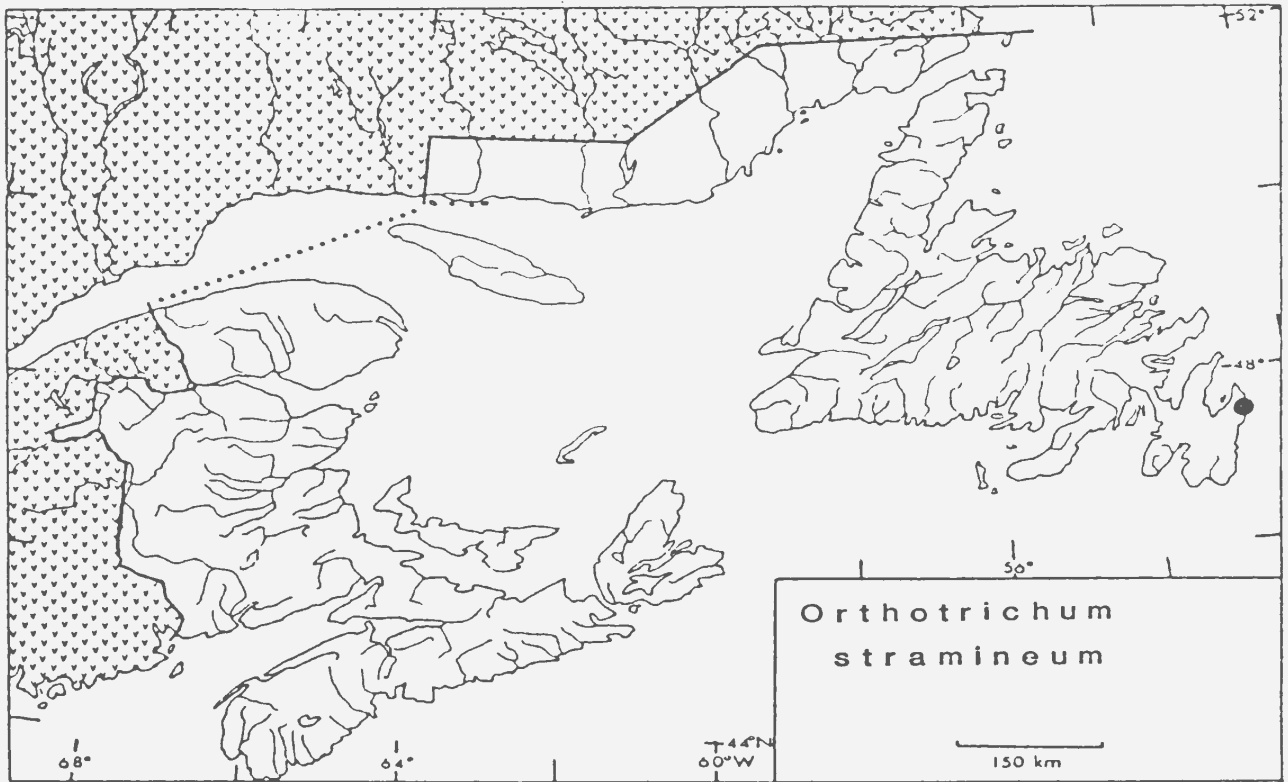


Figure 4-23. The distribution of *Orthotrichum stramineum* in the Gulf of St. Lawrence.

Figure 4-24. The distribution of *Zygodon conoideus* in the Gulf of St. Lawrence (circles with triangles are county reports from Ireland (1982)).



The great majority of bryophytes which migrated from the south have distributions in eastern North America continuous southward to North Carolina and Tennessee, where most are widespread or common. However, several bryophytes have their southern limits in eastern North America just south of Cape Cod, where they are rare: *Pohlia bulbifera* (Ketchledge 1980), *Schistostega pennata* (Crum and Anderson 1981), *Seligeria campylopoda* (Vitt 1976), *Sphagnum angermanicum* (Holcombe 1979), and *Trematodon ambiguus* (Ketchledge 1980).

Many of the bryophytes are also present in the western Great Lakes region (Table 3-3). Most have continuous distributions from this region to the Gulf but five are disjunctive there from the Gulf centre: *Andreaea rothii*, *Buxbaumia aphylla*, *Diplophyllum taxifolium*, *Isopterygium muellerianum*, and *Nardia geoscyphus*.

Ten bryophytes are absent in the western Great Lakes region: *Amphidium mougeotii*, *Campylostelium saxicola*, *Dicranella palustris*, *Ephemerum serratum*, *Grimmia donniana*, *Hygrohypnum montanum*, *Isopterygium tenerum*, *Lejeunea ulicina*, *Pohlia andalusica*, *Sphagnum angermanicum*.

A large percentage of the bryophytes in the migrants from the south group are also present in arctic regions (e.g., sub-elements C1, C2, Table 3-3). Most are found in southern Greenland: however, many are disjunctive from central

Labrador to that region and very few (eight species) have continuous distributions from the Gulf to the arctic (*Cephaloziella leucantha*, *Cladopodiella fluitans*, *Dicranella cerviculata*, *Grimmia donianna*, *Hygrohypnum ochraceum*, *Racomitrium heterostichum*, *Rhytidium rugosum*, *Scapania undulata*).

Four bryophytes included within the 'south' migrants are rare south of the Gulf even though they are continuous to this region by my definition: *Grimmia donniana*, *Hygrohypnum montanum*, *Nardia geoscyphus*, and *Rhytidium rugosum*. *Grimmia donniana* and *Hygrohypnum montanum* have their main area of distribution south of the study area in the Appalachian Mountains where they are rare (Crum and Anderson 1981), and *Nardia geoscyphus* and *Rhytidium rugosum* are widespread arctic bryophytes having their southern limits in suitable localities south of the study area.

The study area is a northern limit in eastern North America (excluding Greenland) for about 51% of the mosses (36 species) and 33% of hepatics (4 species) which migrated from the south. *Pohlia annotina* (Figure 4-25) is a "possible circumtemperate" species common in disturbed habitats (Shaw 1982) that has its northern limit in the study area in eastern North America.

The remaining 40 species, like *Isopterygium elegans* (Figure 4-26) have probably migrated north through the study area and reach their northern limits in central Labrador (55°-56° N lat.) (Brassard and Weber 1978a).

Figure 4-25. The North American distribution of *Pohlia annotina*
(expanded from Shaw (1980); also reported from Greenland).

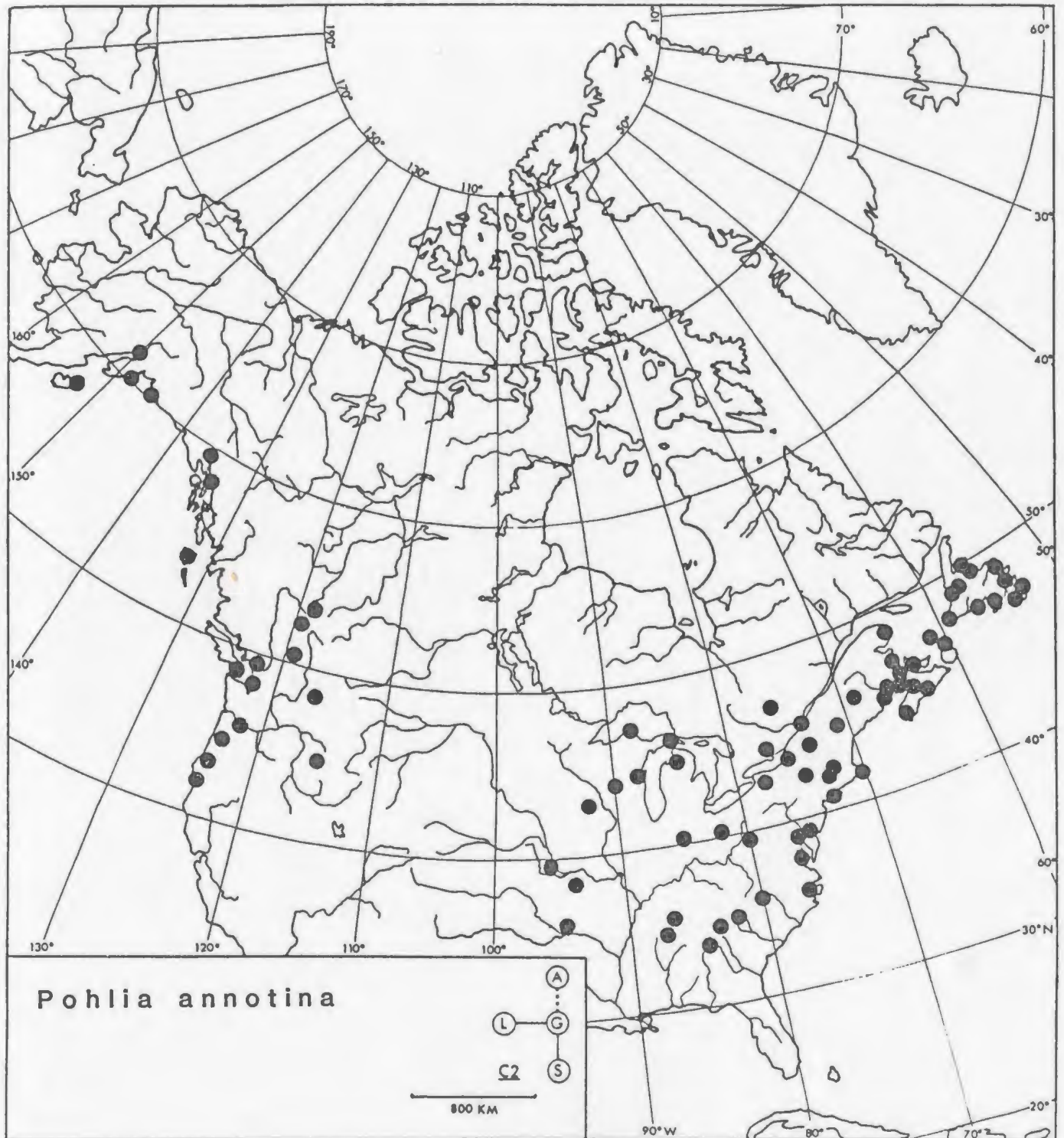


Figure 4-26. The North American distribution of *Isopterygium elegans* (expanded from Ireland (1969);also reported from Greenland).



The general decline of regional diversity northward through the Gulf of species whose main distribution is south of the Gulf (Figures 3-2, 3-3) is one of the best indications of northward migration for these species and is especially evident when considering the very rare or rare bryophytes in the group. Of the 17 species in these frequency classes, 14 occur only south of the St. Lawrence River, e.g., *Aulacomnium heterostichum*, *Isopterygium distichaceum*, and *Lejeunea ulicina*.

Although many bryophytes supporting migration from the south to the study area are disjunct within a portion their eastern North American range, it is probable that these disjunctions are not directly related to the migrational history of the species in the Gulf region. Four sub-elements, for example, have a disjunctive component to either the Great Lakes or to the Arctic. These sub-elements can be paired with sub-elements otherwise showing similar overall patterns of distribution in eastern North America but differing only by the presence/absence of a disjunction. Examples of such non-disjunct/disjunct pairs include C2/C5, C5/C6, and C9/C13. A closer study of such sub-element pairs may give insight as to the relationships between discontinuous and continuous distribution patterns. For instance, species in sub-elements C2 and C5 differ only by the disjunction to the Arctic in sub-element C2. The bryophytes in sub-elements with disjunctions to the Arctic occur mainly in southern Greenland, and are mainly boreal or temperate species. The distribution and ecology in Greenland of vascular plant species of similar boreal and temperate affinity has been discussed by Böcher (1963).

4.2.2. Survivors in Refugia

Survival of plants within the study area during the Last Glaciation is the most controversial of all the histories considered in the present study.

Thirty-six percent of the total disjunct bryoflora (14% of the total Gulf of St. Lawrence bryoflora) have eastern North American distributions supporting the hypothesis of survival in refugia in the Gulf of St. Lawrence region. According to my studies, 96 bryophytes might have survived in glacial refugia within the study area during the Last Glaciation. These are disjunctive to the arctic and/or to the southern Appalachians, or restricted to the Gulf centre (Table 3-7). One would not expect so high proportion of such disjuncts in a region which has experienced total glaciation.

While all such species have eastern North American distributions fitting the criteria for support of survival in refugia, a few species have relatively widespread distributions south and west of the Gulf centre, or have distributions in the study area suggesting anthropogenic introduction. Thus, the following should be excluded from the list of refugial species: *Barbula reflexa*, *Seligeria recurvata*, *Tortula muralis*, *Stokesiella praelonga*. The first three are all disjunctive to the southern Appalachians and to the Great Lakes, but are only slightly or narrowly discontinuous between these latter centres (Crum and Anderson 1981; Vitt 1976). *Tortula muralis* and *Stokesiella praelonga*, may have been accidentally introduced to the Gulf (Brassard 1983c, 1984b).

Six sub-elements support the refugial hypothesis. With the exception of the hypothesis of migration from the south, no other hypothesis considered in this study is supported by such a wide variety of eastern North American distribution patterns. The diversity and complexity of the disjunctions are presumed to reflect the disruption by glacial action of formerly more continuous distributions.

Three-quarters of the bryophytes supporting refugia are disjunctive to the arctic, with slightly more than half of these being disjunctive *only* to this centre (sub-element D5) (Table 3-1). The following discussion (pages 116-126) concerns only this group (sub-element D5).

Refugial species disjunctive only to the arctic can be divided into two groups based on their world distributions, arctic and montane. Arctic species are widespread throughout arctic regions and extend their ranges southwards into suitable habitats in mountain ranges or along coastal barrens and tundras. This definition is equivalent to that of "arctic-alpine" given by Schofield (1969). Montane bryophytes are almost wholly restricted to mountain ranges throughout their world range, and they extend into the arctic only in mountains. This definition differs from Schofield's (1969) "circumalpine element" in that it is slightly broader, including not only species of boreal affinity, but of temperate affinity as well.

In eastern North America, both montane and arctic species show a

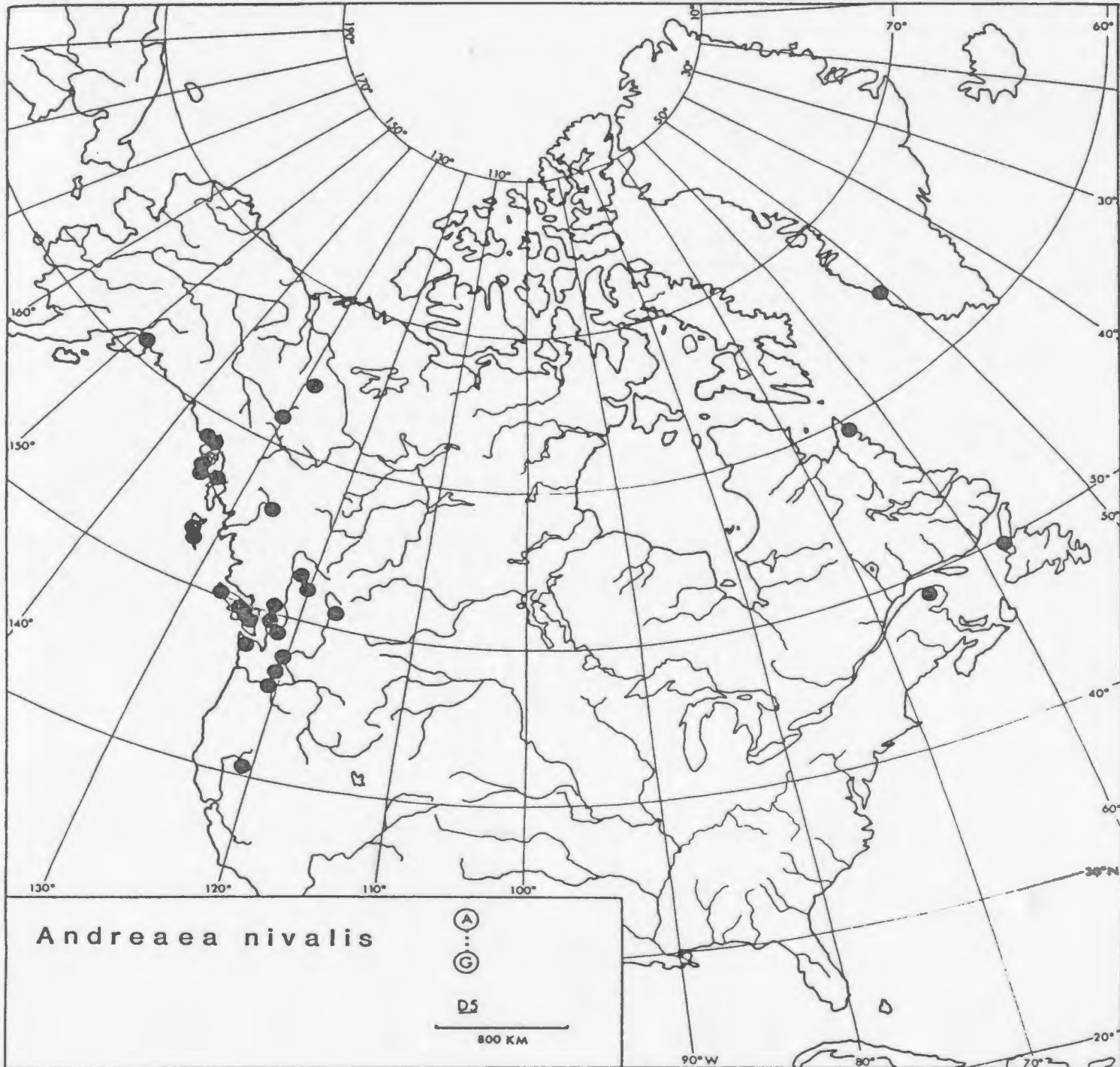
disjunction from the Gulf to the Arctic. However, their distributions within the North American Arctic are quite different.

The 29 montane bryophytes disjunctive only to the arctic from the Gulf have restricted distributions in the Arctic. Thirteen of these species occur in the high arctic (north of 75°N), where most are rare, e.g., *Campylopus schimperi*, *Desmatodon laureri*, *Metacalypogeia schusterana*; only five species occur in the non-mountainous east coast and islands of Hudson Bay, e.g., *Cynodontium strumulosum*, *Hygrobiella laxifolia*, and *Solenostoma obovatum*. The montane bryophytes are also generally absent from the mountains of New England and New York.

Most of the montane disjuncts to the arctic show large disjunctions (>1100 km) from the study area, many having their nearest station either in the mountains of northern Labrador, or along the southwest coast of Greenland. *Andreaea nivalis* (Figure 4-27) is a typical example of a montane moss. This species, known from two localities within the study area, is disjunctive to the Torngat Mountains of northern Labrador, and has one station in west Greenland.

Oedipodium griffithianum has a similar overall distribution as *Andreaea nivalis* in eastern North America (map in Brassard 1983a). However, this species is unknown in Labrador, but is more widespread in southwest Greenland. In the Gulf, *O. griffithianum* has two stations in Newfoundland, where it occurs near

Figure 4-27. The North American distribution of *Andreaea nivalis*
(expanded from Schofield (1972)).



unglaciaded surfaces (Brookes 1977; Grant 1977a). Størmer (1969) suggested that *O. griffithianum* was relictual in Europe. Its extreme disjunction in Newfoundland would support a similar status there.

The close association of the refugial montane bryophytes to coastal mountains, especially in the arctic, is significant. Many of the bryophytes are restricted to areas where geological evidence suggests the existence of ice-free areas during most, if not all, of the Wisconsin glaciations, e.g., the Torngat Mountains (Ives 1978; Rogerson 1981), the east coast of Baffin Island (Ives 1978), Northern Ellesmere Island (England 1978), east and west Greenland (Funder 1978). These ice-free montane areas could have provided an almost continuous 'strip' of coast available for the survival of the montane bryophyte flora during the whole of the Wisconsin (ca. 80,000 years).

As compared to the montane bryophytes, arctic species disjunctive from the Gulf only to the arctic are widespread there. Of the 25 such species, 21 extend into the high arctic, and the majority also reach westward across the North American arctic to Alaska, e.g., *Bryum wrightii* (Figure 4-28), *Hypnum bambergeri*, *Lophozia bantriensis*. Many arctic species show small disjunctions from the Gulf to the arctic and 52% have their nearest Gulf stations on the east coast of Hudson Bay. Their presence in recently deglaciaded territory suggests recent postglacial dispersal, although the source(s) for these populations is not

known. They are possibly derived from populations which survived in southern refugia (including the Gulf of St. Lawrence), but they may also have had their sources from populations surviving in coastal refugia in Labrador or in arctic refugia.

Some arctic species, however, have large disjunctions from the Gulf to the arctic. *Stegonia latifolia* (Figure 4-29) has one known station in the Gulf, at St. John Highlands, western Newfoundland. Its nearest station in North America is northern Baffin Island, a disjunction of ca. 2,600 km. *Hypnum procerrimum* (mapped by Schofield 1972) has a similarly wide disjunction from the Gulf to the arctic.

Seven of the arctic bryophytes belong to the High Arctic Element (Steere 1965, 1979; Brassard 1971, 1974): *Bryum wrightii*, *Cyrtomnium hymenophylloides*, *Desmatodon leucostomus*, *Didymodon asperifolius*, *Lophozia binsteadii*, *Scapania hyperborea*, *Tortella arctica*. Their occurrence in the study area is of considerable interest especially since Steere (1965, p. 487) states that "...populations in the Alps and in the Rocky Mountains...may be relics of the Quaternary glaciation". My studies suggest that they may also be relics of the Last Glaciation in the Gulf. Several of the high arctic species display the largest disjunctions of the arctic refugial group, e.g., *Desmatodon leucostomus*, *Didymodon asperifolius*, *Tortella arctica*.

Figure 4-28. The North American distribution of *Bryum wrightii*
(expanded after Steere and Murray (1974)).

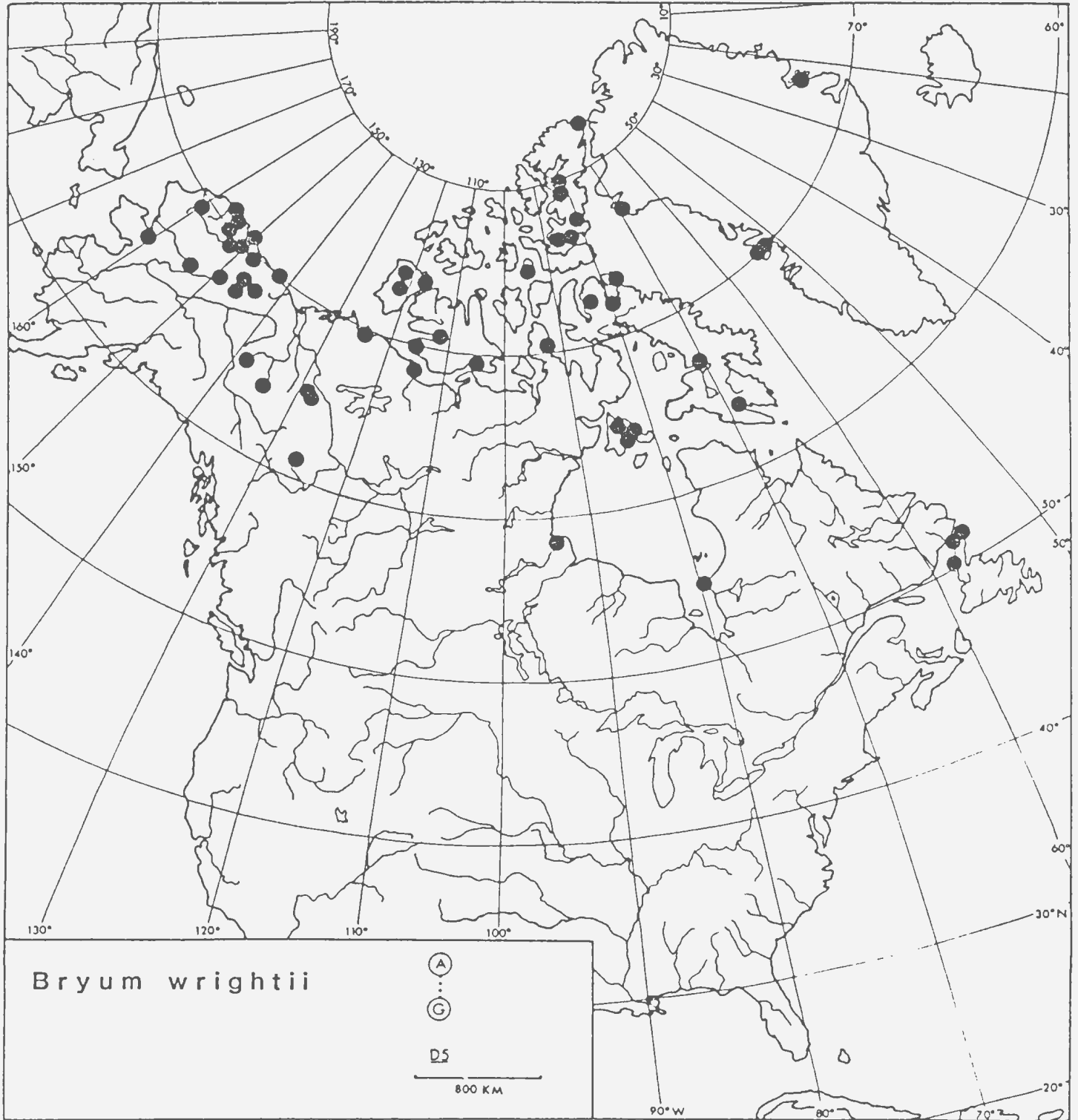
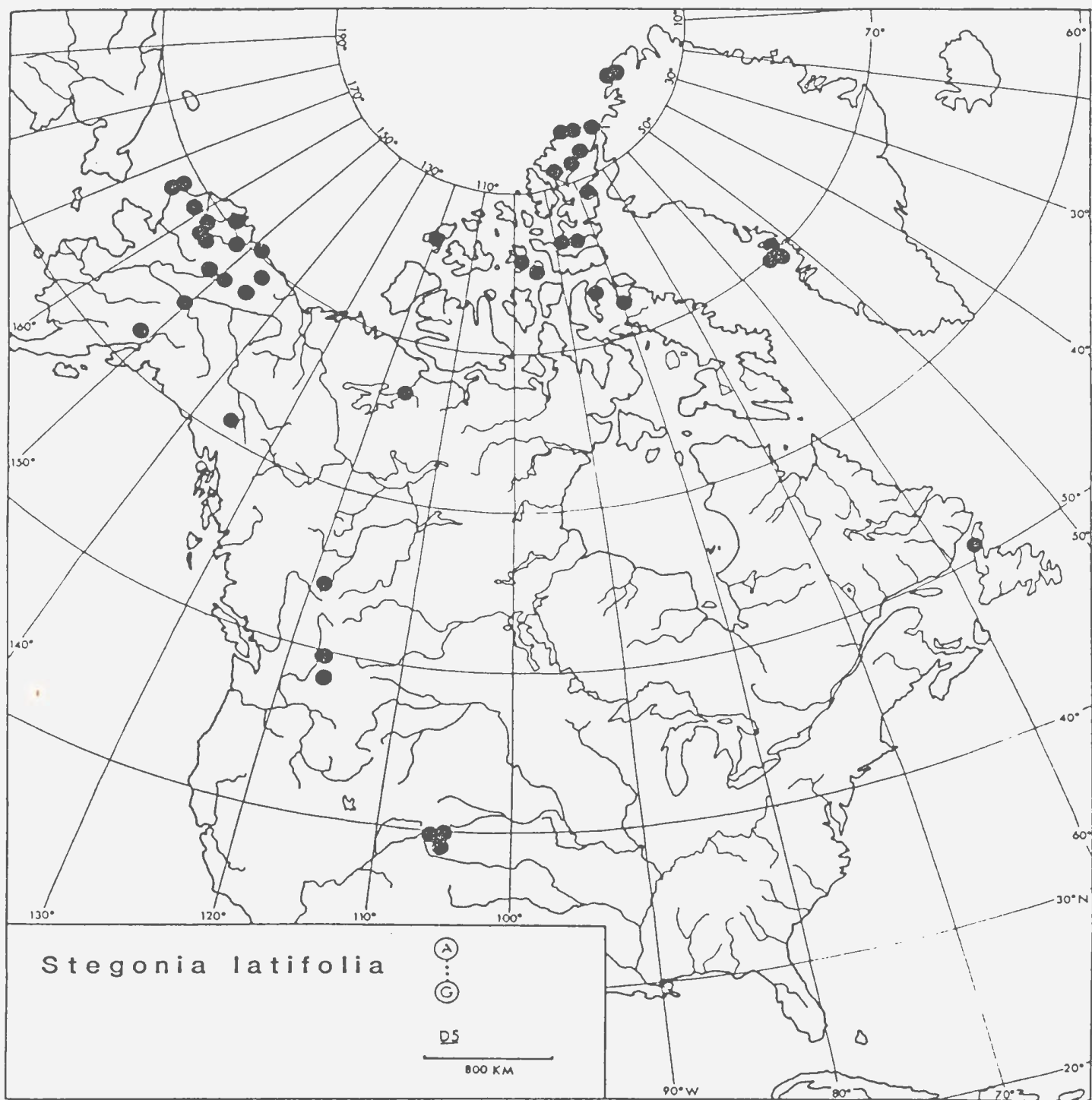


Figure 4-29. The North American distribution of *Stegonia latifolia*.



Many of the refugial bryophytes may be absent between the Gulf and the arctic because of lack of collecting (as compared to other regions) in intervening regions, and it is possible that many of the 'D5' species will eventually show 'C10' distributions. However, many collections have been made in Labrador (Brassard and Williams 1975; Brassard and Weber 1978a), and the general pattern of distributions north of the study area are basically known.

Several boreal species are disjunctive from the Gulf only to the arctic: *Antitrichia curtispindula*, *Brachythecium collinum*, *Cladopodiella francisci*, *Harpanthus flotovianus*, *Rhytidiadelphus loreus*, *Seligeria diversifolia*, *Splachnum sphaericum*. Except for *Cladopodiella francisci*, these are disjunctive from the Gulf centre only to southern Greenland. Within the Gulf centre, three are restricted to the study area (*Antitrichia curtispindula*, *Brachythecium collinum*, *Seligeria diversifolia*), and thus show large disjunctions to the arctic. The large disjunctions of these boreal species are particularly critical since they might be expected to occur more continuously through the boreal zone of Quebec-Labrador.

Of the bryophytes with disjunctions from the Gulf of St. Lawrence to the southern Appalachians (Table 3-2, page 52) seven are disjunctive only to that region (sub-element D6). A few of these have disjunctions to areas just beyond the southern limits of the Gulf centre (*Bryum alpinum*, *Campylium halleri*, *Philonotis yezoana*) where they are rare (Crum and Anderson 1981).

Of the species disjunctive only to the southern Appalachians, three have disjunctions greater than 1500 km: *Campylopus atrovirens*, *Entodon concinnus*, and *Herberta adunca*. Their possible glacial survival in this area has been previously mentioned (Belland 1981; Brassard and Hooper 1981; Brassard 1983a, 1984b). These species are discussed individually below since they provide particularly strong support for survival in the Gulf during the Last Glaciation.

Herberta adunca has its widest distribution south of the study area where it ranges from the Catskill Mountains of New York, southward to South Carolina and Georgia (Schuster 1974). Its limit in the Catskill Mountains, and almost entire restriction to the unglaciated south is highly indicative of its relictual status there. Only two stations for *H. adunca* are known in the Gulf and these represent a disjunction of ca. 1500 km from the Catskill Mountain populations. Both Gulf stations occur on the south coast of Newfoundland near probable unglaciated areas (Leckie and McCann 1983). The wide disjunction from the southern populations, the rarity of the species in the Gulf, and the proximity of the known Gulf populations to possible unglaciated strongly suggests that *H. adunca* was a glacial relic in the Gulf also.

In contrast to *Herberta adunca*, *Entodon concinnus* and *Campylopus atrovirens* have numerous populations in parts of the Gulf, but are otherwise known in eastern North America from one or two localities in the mountains of North Carolina and Tennessee (Crum and Anderson 1981).

Campylopus atrovirens is an oceanic species (Tuomikoski *et al.* 1973; Crum and Anderson 1981; Frahm 1980), that, in much of its world range grows at low elevations on wet acidic rock faces (Frahm 1980). This might explain its restriction in the Gulf mainly to the relatively more oceanic south coast of Newfoundland where it is quite frequent (Brassard 1983a) in such habitats. However, the ecology of this moss appears to vary throughout its world distribution. In western Newfoundland *C. atrovirens* also grows (more rarely) at higher elevations on basic rocks (Belland 1981), and in the Alps and Turkey, it grows on high exposed sites, rich in calcium (Størmer 1969). The variable ecology of *C. atrovirens* would favor a larger distribution for the species in the study area and in eastern North America. Poor dispersal ability may be a factor explaining the limited distribution of the species, as has been suggested for the species in Sweden (Bohlin *et al.* 1980). *C. atrovirens* fruits very rarely anywhere in its world range, and reproduces primarily by deciduous leaves and leaf tips (Frahm 1980). Thus, the species' distribution in the Gulf of St. Lawrence could be explained by limited postglacial migration from southern Newfoundland or Grand Banks refugia, where (sub)oceanic conditions would prevail even during a glaciation.

Further support for the refugial status of *Campylopus atrovirens* is provided by *Entodon concinnus*, which has an overall distribution similar to that of *C. atrovirens* in eastern North America, but is not considered oceanic. Its

North American distribution (map in Brassard 1983a) strongly suggests that it survived the Last Glaciation in four centres, all of which are thought to have had ice-free areas during the Last Glaciation: Colorado, Beringia, the southern Appalachians, and Newfoundland and Cape Breton Highlands.

Like *Campylopus atrovirens*, *Entodon concinnus* also has a variable ecology. In the Gulf of St. Lawrence region, *Entodon concinnus* has been found on acid rocks as well as on calcareous rocks; it is known from exposed coastal sites and also from forested localities and high altitudes. Its frequency and abundance in western Newfoundland suggests a relictual distribution in the Gulf. Like *Campylopus atrovirens*, *E. concinnus* is only known sterile in North America (Crum and Anderson 1981) suggesting a very limited dispersal ability for the species here.

Six bryophytes in the refugial group are disjunctive *only* from the Great Lakes to the Gulf in eastern North America, and, although not found in the arctic, these might provide equally good evidence for western migration to the Gulf : *Bryum miniatum*, *Cephalozia affinis*, *Grimmia tenerrima*, *Hygrohypnum bestii*, *Isothecium alopecuroides*, *Scapania umbrosa*. *Cephalozia affinis* (Schuster 1974) and *Isothecium alopecuroides* (Allen 1983) are rare or absent in western North America, and the Cordillera is unlikely to have been the source for the eastern North American populations. However, it has been

suggested for *Hygrohypnum bestii* and *Scapania umbrosa*, that the populations in the Great Lakes may have originated from populations surviving glaciation in the Driftless Area of Wisconsin and Minnesota (Schuster 1958a, 1958b, 1984). As support for this idea, Schuster (1958a, 1958b) used the small disjunctions of some species between the Driftless Area and the Great Lakes to suggest postglacial migration from the Driftless Area to the latter region. Of the species listed above, only *Bryum miniatum* is presently known from the Driftless Area, although it is absent from the Great Lakes. Whether any of these species were widespread in a tundra corridor is difficult to evaluate; this problem is addressed in more detail in a further section (page 146).

Sixteen species supporting refugia are present only in the Gulf centre (sub-element D8 in part) and 12 are restricted to the study area. Most are widespread there, but four are known from only one locality: *Bryum warneum* (Shaw and Marcotte 1983), *Cynodontium jenneri* (Tuomikoski *et al.* 1973), *Myrinia pulvinata* (Crum and Anderson 1981), and *Trematodon montanus* (Belland and Brassard 1983). *T. montanus* (Figure 4-30) is a recently described moss species and it is the rarest of all the disjuncts treated in this study. It is presently known from only two localities in North America (and the world): one on the Long Range Mountains of western Newfoundland, and one from the Queen Charlotte Islands. Both areas are likely to have had ice-free areas during the Last Glaciation (Grant 1977a; Warner and Mathewes 1982). The extreme rarity and disjunction (ca.

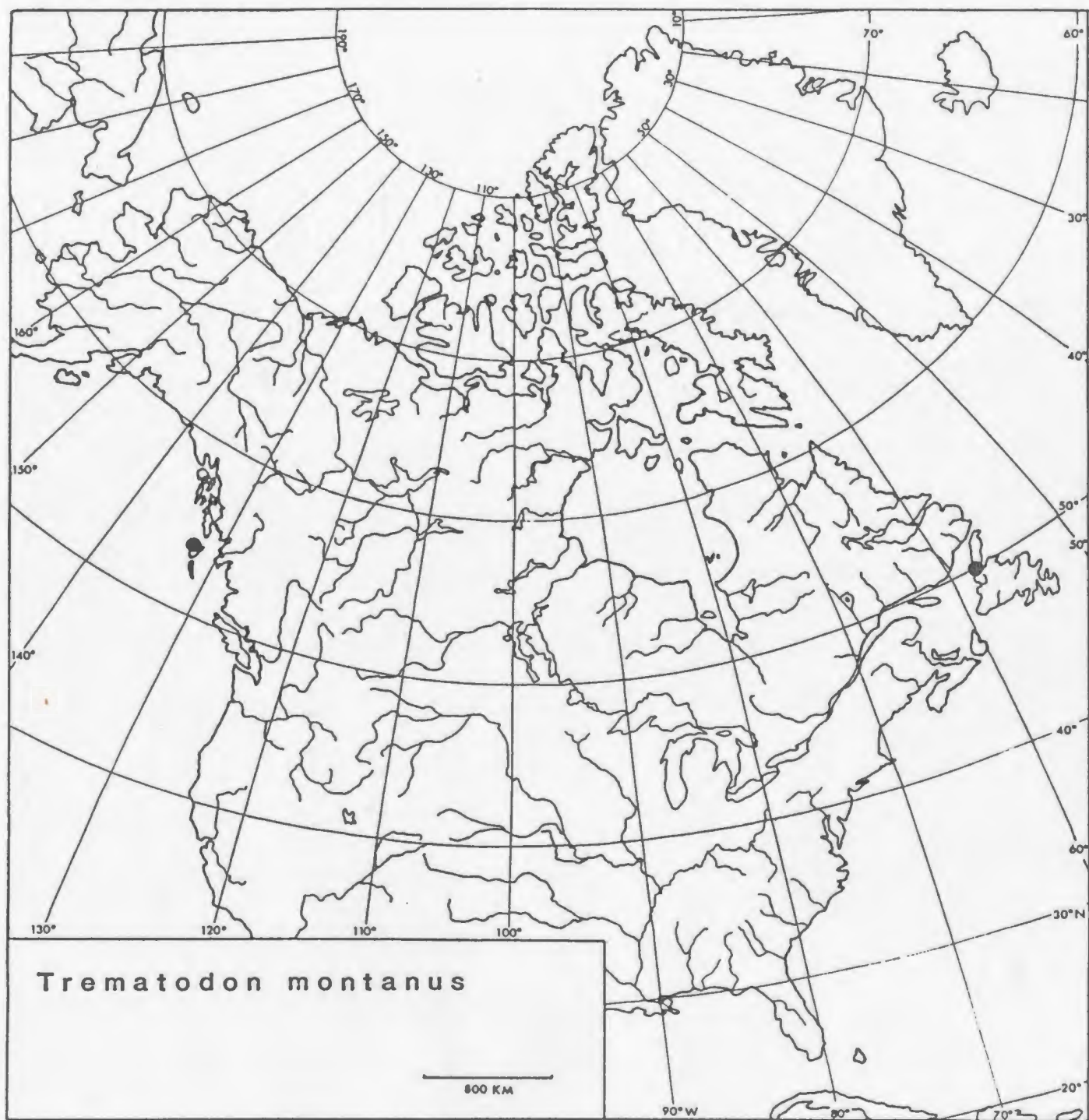
4,900 km) of *T. montanus* and its presence only near possible Wisconsin ice-free areas strongly suggests a glacial relic status for this species.

The four (of the 16) species restricted to the Gulf centre but which have distributions extending outside the study area (*Dicranum leioneuron*, *Seligeria tristichoides*, *Tetraphis geniculata*, *Ulota phyllantha*) are all boreal species present south and/or north of the study area, where they are rare (Forman 1962; Vitt 1976; Brassard and Weber 1978a; Crum and Anderson 1981). However, within the study area, these species are mostly common and widespread.

Species best supporting the refugial hypothesis will show little migration from possible refugia since glaciation; thus many of the refugial species should be restricted to the study area. More than half, 55% (53 species), of the disjunct bryophytes supporting refugia in the study area are found *only* within the study area within the Gulf centre.

The restriction of these species might be explained by lack of suitable habitats north and south of the study area but the species occupy a wide range of habitat types, from forest and open lowland communities (e.g., *Orthotrichum gymnostomum*) to alpine tundra (e.g., *Trematodon montanus*). Several regions outside the study area (southern Labrador, New England/New York) are known to have suitable habitats, and there seems to be no obvious reasons why most of the bryophytes restricted to the study area could not be found there also. In

Figure 4-30. The North American distribution of *Trematodon montanus* (after Belland and Brassard (1983)).



particular, it is difficult explaining the absence of montane and arctic bryophytes from coastal tundra areas in southern Labrador, e.g., *Desmatodon leucostomus*, *Hypnum bambergeri*, *Orthothecium chryseum*, *Sauteria alpina*, *Scapania uliginosa*.

The absence of 66% of the refugial species in New England and New York, both of which are particularly well known bryologically, is noteworthy. Surely, if the presence of the refugial disjuncts in the study area were the result of postglacial migration through or from these states, then a higher percentage should still be present there. The presence of boreal and temperate species, common in some regions within the study area (e.g., *Homalothecium sericeum*, *Orthotrichum gymnostomum*, *Ulotia drummondii*) but absent in New England/New York is especially remarkable since there seems to be no evident reasons why such species should be absent in those regions.

It is also noteworthy that only a few disjunct bryophytes have isolated populations in New England/New York but are *absent* from the Gulf: *Haplomitrium hookeri*, *Hookeria acutifolia*, *Scapania spitzbergensis*. This lack of critical disjuncts south of the study area only serves to emphasize the importance of the Gulf as a possible ice-free refugium.

Some of the arctic and montane species may have become extinct postglacially south of the study area because of ameliorating climate and the

consequent decrease in area of suitable open habitats south of the study area. However, there is little to suggest that many of the refugial species presently restricted to the study area were ever present in regions to the south in the refugial group. So far only one species in the refugial group, *Hypnum bambergeri*, is known as a sub-fossil, from lateglacial deposits in Wisconsin (Miller 1980a, 1980b). *H. bambergeri* is today a widespread species in the arctic, and its distribution includes the glaciated areas near Hudson Bay. Clearly, this species is easily dispersed and thus its wide distribution during the lateglacial is understandable.

4.2.3. Disjunct Bryophyte Migration from the North

Postglacial migration of bryophytes from the north has only recently been proposed to explain some bryophyte distributions in the the Gulf of St. Lawrence region (Brassard 1984a). Relatively few (26) disjunct bryophytes support this hypothesis. All the bryophytes supporting migration from the north are continuous from the arctic to the study area. Only *Brachythecium turgidum* and *Distichium inclinatum* extend sporadically westwards to the Great Lakes.

Fifteen species which may have migrated from the north reach their southern limits in eastern North America in New England or in New York state, but of these only *Schistidium maritimum* is common there (Bremer 1980a). The remaining bryophytes are restricted primarily to the Appalachian Mountains,

where three are known from a single locality: *Lescurea saxicola* (Lawton 1957), *Plagiobryum zierii* (Crum and Anderson 1981), and *Pohlia obtusifolia* (Shaw 1982).

Eleven bryophytes which may have migrated from the north reach their southern limits in eastern North America within the study area: *Andreaea blyttii*, *Brachythecium turgidum*, *Calliergon wickesiae*, *Desmatodon latifolius*, *Dicranum angustum*, *Drepanocladus badius*, *Kiaeria falcata*, *K. glacialis*, *Pleuroclada albescens*, *Polytrichastrum sexangulare*, *Tritomaria polita*.

The generalized eastern North American distribution of species in this group would seem to support the explanation of the species having migrated from the arctic to the study area postglacially. It seems reasonable to assume that bryophytes which might have migrated to the Gulf from the north should be common and widespread in the eastern North American arctic. A close study of the species in the migrants from the north group shows, however, that only half of the species in the group are common and widespread in that region. These all occur in the high arctic, and many reach the east coast of Hudson Bay, e.g., *Dicranum elongatum*, *Drepanocladus badius*, and *Gymnomitrium corallioides*.

The others are unlikely to have migrated to the Gulf from the arctic since they have their *main centre* of distribution in the mountains of northeastern North America. When present in the arctic, they occur mainly in low eastern

arctic, e.g., *Andreaea blyttii* (Figure 4-31), *Calliergon wickesiae* (Figure 4-32), *Polytrichastrum sexangulare*; only three of them have rare extensions into the northernmost latitudes, e.g., *Plagiobryum zierii* (Holmen 1960), *Pohlia drummondii* (Shaw 1982), and *Pleuroclada albescens* (Schuster 1974) and only about one third reach the east coast of Hudson Bay (e.g., *Andreaea blyttii*, *Calliergon wickesiae*, *Distichium inclinatum*, *Kiaeria blyttii*).

Calliergon wickesiae (Figure 4-32) provides a good example of a species in the migrants from the north group which probably did *not* follow this history. In eastern North America, the species has its southern limits in Newfoundland and ranges northward as far as 78°N. However, *C. wickesiae* is much more frequent in the southern portion of its range and cannot be considered an arctic species. Its overall North American distribution suggests a boreo-montane pattern.

One might expect that species with widespread arctic distributions and those not so distributed would both show a pattern of gradual decline southwards through the study area if they had migrated from the north (analogous to the decline northwards of migrants from the south). The regional diversities of both groups within the Gulf (Figures 4-33, 4-34) shows neither group to have such a clear pattern of decline, and that both groups show lower than expected diversities in southern Labrador. Also, the non-arctic species (Figure 4-34) are less well represented in southern Labrador than the species common in the arctic

Figure 4-31. The North American distribution of *Andreaea blyttii*
(expanded from Schofield (1972)).

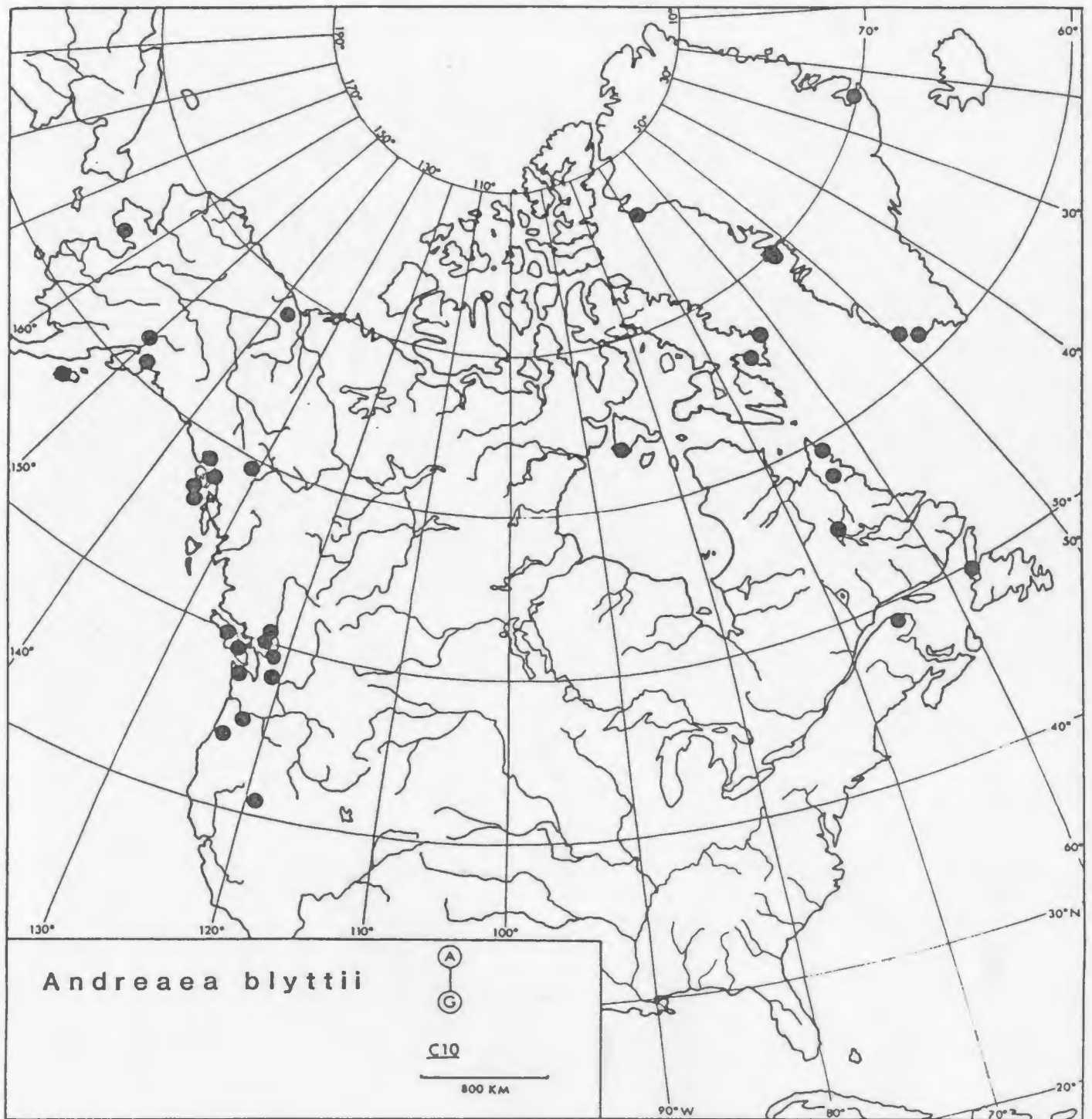
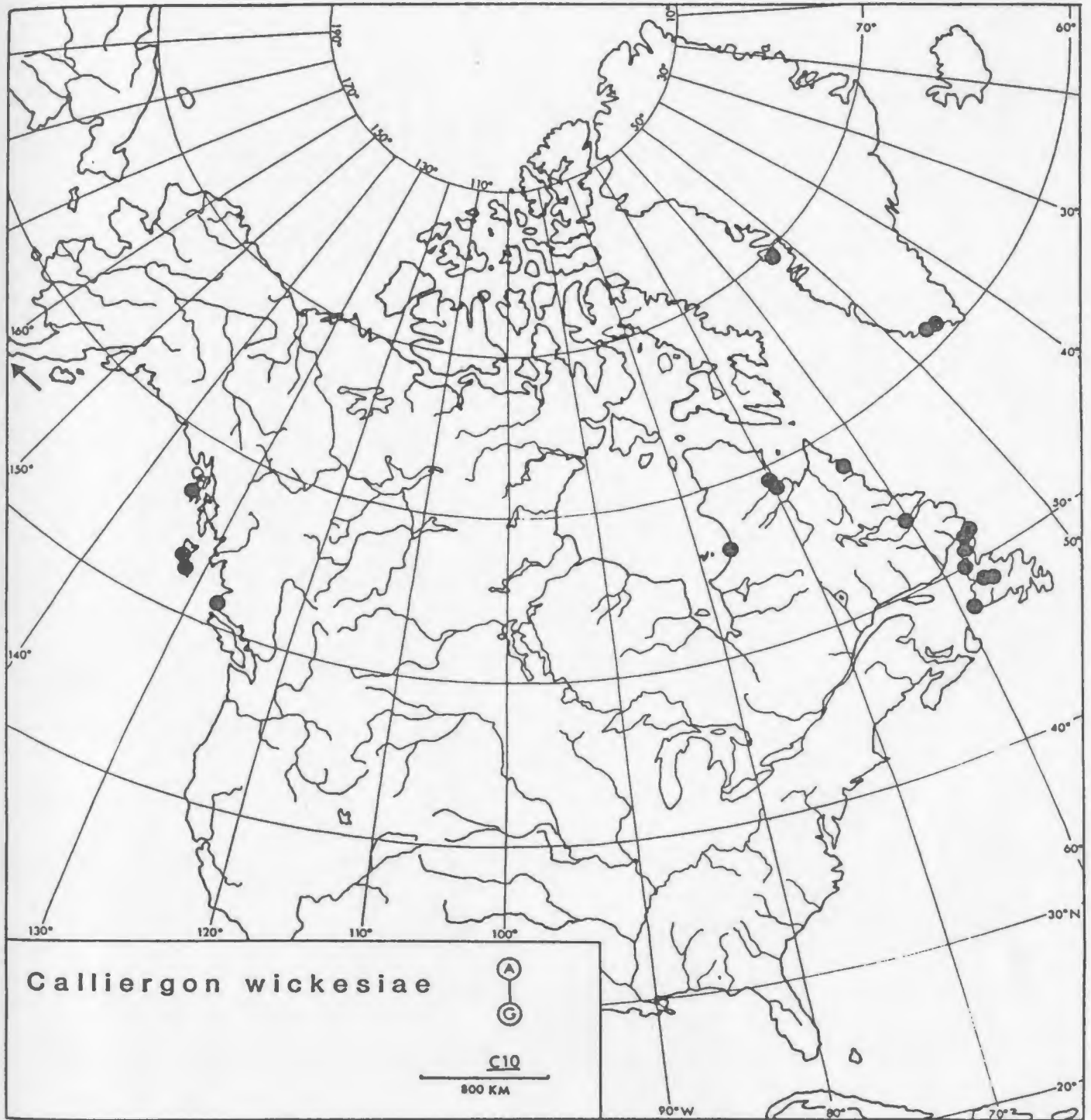


Figure 4-32. The North American distribution of *Calliergon*
wickesiae (expanded from Schofield (1980)).



(Figure 4-33). These results may indicate that the bryophytes in the migrants from the north migrational/dispersal group, and especially the non-arctic species in this group, may be best explained by some other hypothesis (see page 160 for further discussion).

Fifty-four percent of the species widespread in the arctic are in New England/New York, and the possible source for the Gulf populations may have been there. Although neither species is known from late-glacial subfossil assemblages in those regions, the presence of *Brachythecium turgidum* and *Calliergon sarmentosum* as subfossils in late-glacial deposits from Wisconsin and Minnesota (Miller 1980b) would suggest a wider distribution for these species south of the icesheet in the postglacial times.

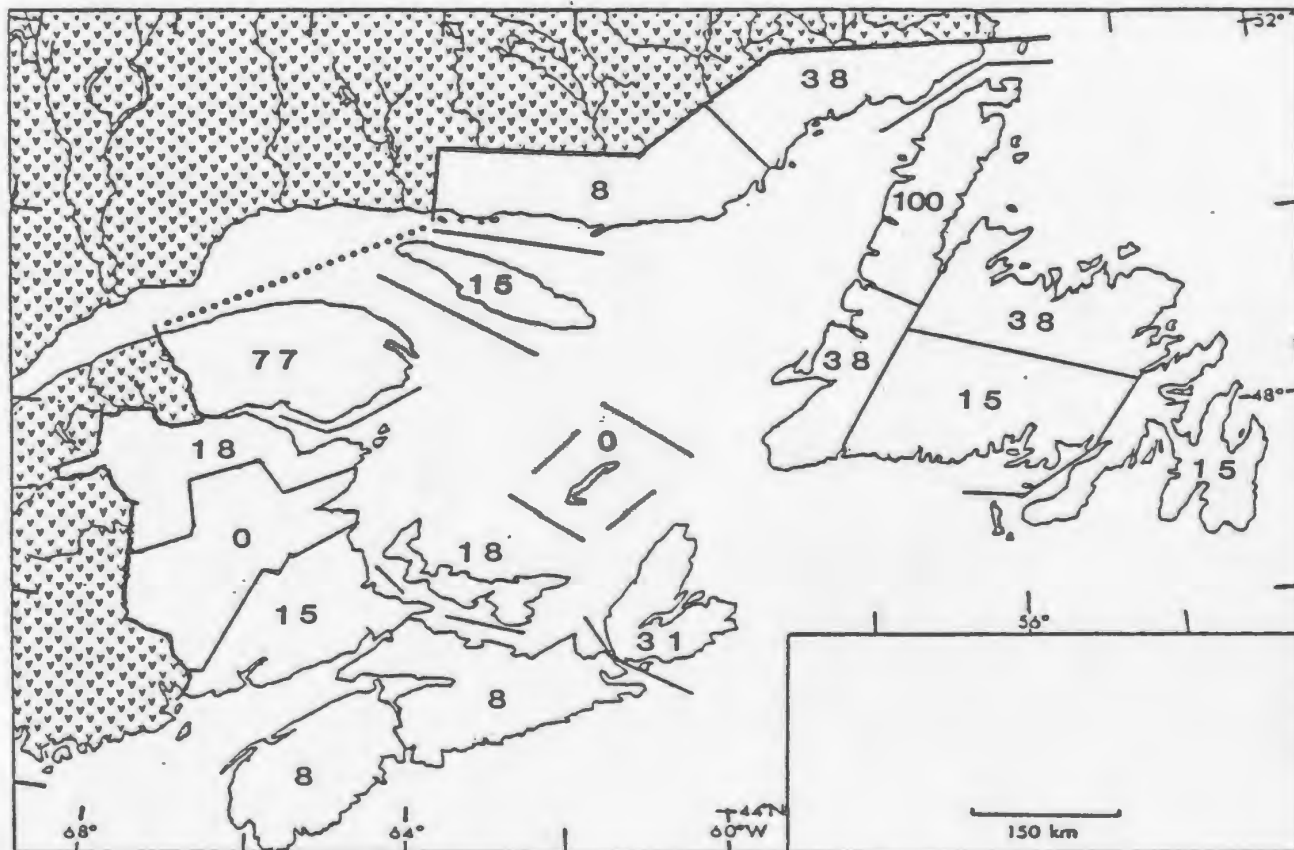
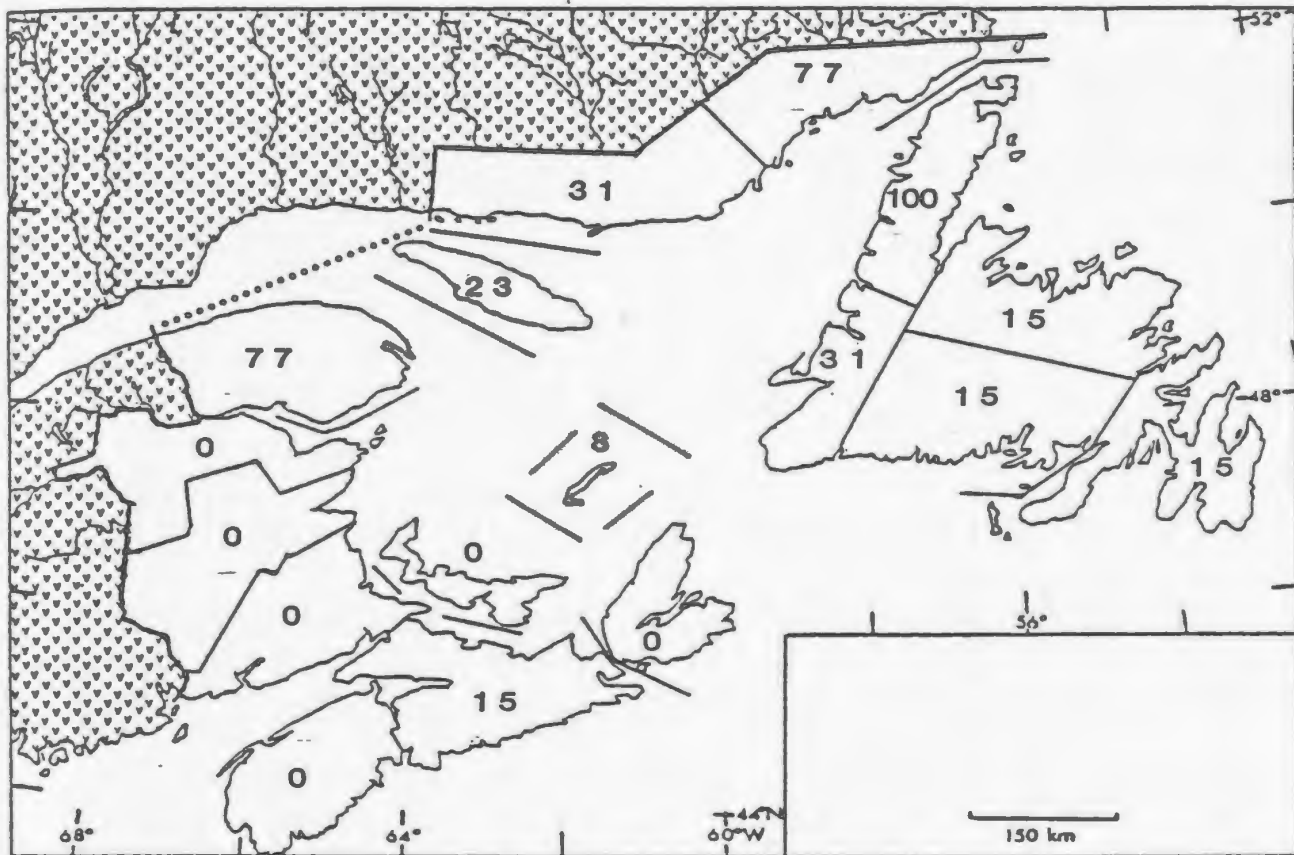
4.2.4. Disjunct Bryophyte Migration from the West

There are no bryophytes whose eastern North American distributions support *only* the hypothesis of migration from the west. Two groups of bryophytes (20% of the disjuncts, 51 species) which might support this hypothesis can also be assigned to other migrational histories (migrants from the north and/or west, and migrants from the west and/or survival in refugia) based on their continuity/disjunction to either the southern Appalachians or arctic. All the species in both groups are present in the arctic (Tables 3-5, 3-6); within the group also supporting survival in Gulf refugia, the species are disjunct to the arctic

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Figure 4-33. The percentage of the arctic species which migrated to the Gulf from the north that occur in the Gulf of St. Lawrence regions.

Figure 4-34. The percentage of the non-arctic species which migrated to the Gulf from the north that occur in the Gulf of St. Lawrence regions.



region whereas in the group also supporting migration to the Gulf from the north the species are continuous to the arctic. A small proportion of species within both groups are also present in the southern Appalachians. However, all species are disjunctive to the Great Lakes, and it is this disjunction on which is based probable migration from the west (or contraction from a wider range along the icesheet margin).

Except for *Calliargon trifarium* and *Catoscopium nigrum*, most species in the migrants from the north and/or west group are disjunctive to the three western Great Lakes, where the majority are rare. Several have been reported from only one or two stations: *Anastrophyllum saxicola* (Schuster 1969), *Anthelia juratzkana* (Schuster 1974), *Chandonanthus setiformis* (Schuster 1969), *Dicranum majus* (Ireland and Cain 1975), *Grimmia torquata* (Schofield 1972), *Hygrohypnum alpestre* (Crum and Anderson 1981), *Myurella tenerrima* (Ireland and Bellolio-Trucco 1979), and *Timmia austriaca* (Brassard 1980). *Calliargon trifarium* and *Catoscopium nigrum* have narrow Great Lakes/Gulf disjunctions, both species being present near Lake Ontario or Lake Erie.

Similarly, most of the bryophytes in the migration from the west and/or refugial group have restricted distributions in the Great Lakes region, where several are known from only one or two localities, e.g., *Dryptodon patens* (Crum and Anderson 1981), *Marsupella sparsifolia* (Schuster 1974), *Orthotrichum*

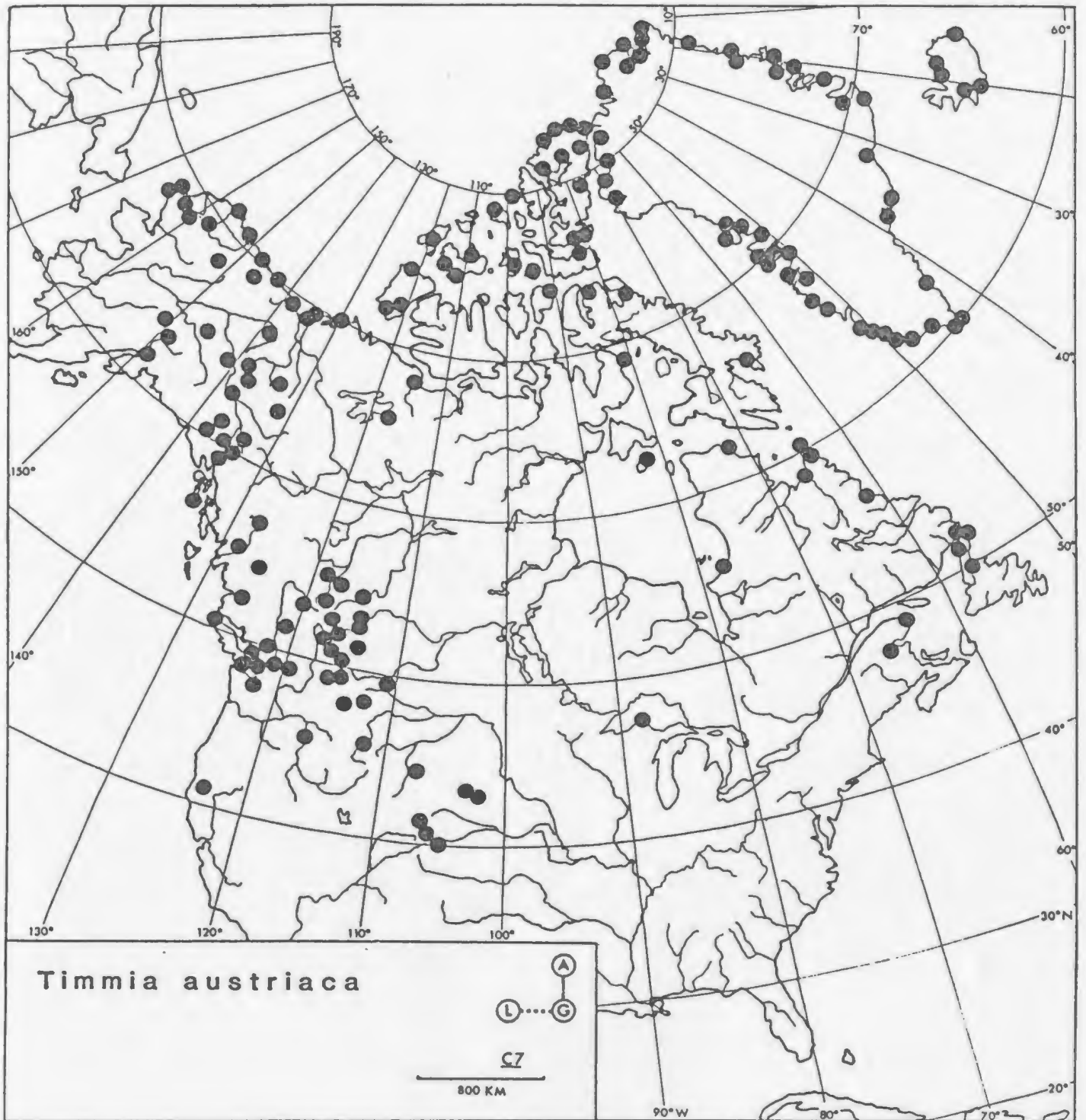
pallens (Miller and Vitt 1970), *Trichodon cylindricus* (Ireland 1978). *Grimmia anodon* and *Gyroweisia tenuis* have larger distributions there (usually southwards) but are nevertheless rare in the Great Lakes region. *Clevea hyalina* is not disjunct from the Gulf to the Great Lakes, but rather to the Driftless Area of Wisconsin and Minnesota (Schuster 1958a).

Of the hypotheses used to explain the presence of disjunct plants at the Great Lakes and in the Gulf of St. Lawrence region, the evidence shown by the disjunct bryophytes for postglacial migration eastwards in a tundra corridor is weakest. This hypothesis assumes that all of the eastern populations originated from western Cordilleran populations during postglacial time; thus the bryophytes should show generally larger areas of distribution in the west as compared to the east. However, 31% of the bryophytes with disjunct occurrences from the Gulf of St. Lawrence to the Great Lakes have continuous distributions from the study area to the arctic (sub-elements C4, C7), and a relatively large proportion are relatively widespread in northeastern North America (e.g., *Aulacomnium turgidum*, *Catoscopium nigrum*, *Barbilophozia hatcheri*, and *B. lycopodioides*). Furthermore, 34% of the species disjunct to the arctic (sub-elements D1, D2) have their main centre of distribution in the arctic and not in the Cordillera (e.g., *Amblyodon dealbatus*, *Lophozia quadriloba*, *Scorpidium turgescens*). It is therefore more reasonable, or equally reasonable, to believe that the present populations in the Gulf may have originated from populations that migrated postglacially to the Gulf from the north rather than from the Cordillera.

Based on distributions alone there is no reason to believe that many (if any) of the Gulf disjunct bryophytes migrated eastwards postglacially along a tundra corridor. However, there is good evidence that some species with Great Lakes-Gulf disjunctions had a wider distribution in the east *during* glaciation. Four species have been found as subfossils in intermediate sites dating from the late-glacial period (11,500-12,100 yrs B.P.) (Miller 1980a): *Aulacomnium turgidum*, *Catoscopium nigrum*, *Scorpidium turgescens*, *Timmia austriaca*. According to Miller (1980a) they grew on recently deglaciated surfaces close to the ice margin. It is significant that all are widespread species in the arctic (e.g., *Timmia austriaca*, Figure 4-35) and presently show only narrow disjunctions from the Gulf to the arctic. If these are representative of the types of bryophytes present in a tundra corridor during glaciation, then only about 46% of the Gulf bryophytes with Great Lakes-Gulf disjunctions might have been present and widespread in the tundra corridor. The remaining species are neither common, nor widespread in the arctic and it is uncertain whether they ever existed in an eastern North American tundra corridor during the last glaciation.

Some inconspicuous bryophytes, e.g., *Cephalozia loitlesbergeri* and *Gyroweisia tenuis*, which are disjunct from the Gulf to the Great Lakes may be undercollected in intervening regions.

Figure 4-35. The North American distribution of *Timmia austriaca*
(expanded from Brassard (1980)).



4.2.5. Introductions by Man

The study area distributions of the following species would support their having been introduced by man to this region: *Orthotrichum stramineum*, *Thuidium tamariscinum*, *Pseudoscleropodium purum*, *Zygodon conoideus*. The four species have been recently discussed in papers by Brassard (1983c, 1984b) and their ecologies and distributions in the study area are discussed below.

Orthotrichum stramineum, *Pseudoscleropodium purum* and *Thuidium tamariscinum* are all restricted to eastern Newfoundland (Tuomikoski *et al.* 1973; Brassard *et al.* 1976; Brassard 1983b) in the Gulf. All three species are reported from St. John's and all can be found in Bowring Park (Brassard 1983c, 1984b). At Bowring Park, the habitats of all three mosses strongly indicate introduction. *Orthotrichum stramineum* grows on planted trees which are mainly of European origin. This moss has also been found on introduced trees elsewhere in St. John's. *Pseudoscleropodium purum* and *Thuidium tamariscinum* grow in shaded lawns in Bowring Park. Only *T. tamariscinum* is known from natural vegetation in Newfoundland at a site in southeastern Newfoundland (Brassard *et al.* 1976).

The North American distributions of the species are similar to patterns described by Lindroth (1957) for introduced beetles. He noted that introduced elements often show restricted distribution in eastern North America and in the

region of Seattle and Vancouver in western North America. Both *Thuidium tamascinum* and *Orthotrichum stramineum* are restricted to the eastern part of the continent, but *Pseudoscleropodium purum* occurs in western North America (Vancouver, Seattle, and a few other localities) where it is also thought to be adventive (Schofield and Crum 1972).

Zydodon conoideus is known from one locality in Newfoundland (Tuomikoski *et al.* 1973) and has been reported from five counties in Nova Scotia (Ireland 1982). The Newfoundland locality is today within the city of Corner Brook and is probably the result of accidental introduction. Although Corner Brook is not considered an important point of entry, Lindroth (1957) has discussed certain ports in western Newfoundland, including Corner Brook, which may have been points of arrival for ground beetles. The species' presence in Nova Scotia, where it seems to be more common, is more difficult to explain. Its habitat there is beech and maple trees (Ireland 1982), presumably within natural vegetation. It is difficult to evaluate whether or not the species was introduced to Nova Scotia judging only by the habitat. Vitt (1970) noted that *Z. conoideus* is dioicous and not known to fruit in eastern North America and, on this basis, suggested that only one sex of the species had been introduced to this continent. If so, then one could expect that the species will be found in suitable anthropogenic habitats.

4.2.6. Natural Long Distance Dispersal

No disjunct bryophytes whose eastern North American distribution suggests arrival to the Gulf via long distance dispersal had diaspore sizes supporting this hypothesis. The results presented (Appendix C) suggest that small (<25 μm) and large (>25 μm) diaspores are equally well represented among bryophyte disjuncts to the Gulf and species which are continuous to the Gulf.

Since disjuncts in the study area are *not* better represented by species with greater potential for long distance dispersal as measured by diaspore size, then one would conclude that, for the Gulf of St. Lawrence disjunct bryophytes, other hypotheses provide better explanations for their presence there. These results are in accord with Crum (1972) who stated that, for the Great Lakes mosses, historical factors and stepwise dispersal adequately explains the composition of the bryoflora in that region.

4.2.7. Unexplained Bryophytes

The migrational/dispersal histories of 12 bryophytes cannot be explained by the hypotheses outlined earlier. These belong to two sub-elements having similar distribution in eastern North America. All have continuous distributions to the Great Lakes from the Gulf of St. Lawrence; eight species are discontinuous to the arctic, and four are continuous to this region.

The continuous distributions of all the unexplained species to the Great

Lakes coincides almost wholly with the Great Lake-St. Lawrence forest region (Rowe 1977), and it would appear that most species are centred on this forest zone, e.g., *Rhizomnium magnifolium* (map in Koponen 1973) and *Tetrodontium brownianum* (map in Schofield and Crum 1972). Most of the unexplained species probably migrated into the Gulf from the south postglacially, following the northward migration of the Great Lakes-St. Lawrence forest belt (Delcourt and Delcourt 1981; Delcourt *et al.* 1983).

4.3. General Discussion

In the previous section, I discussed the distributions of bryophytes within migrational/dispersal groups at two geographic levels, the Gulf of St. Lawrence, and eastern North America. In the present section, I will compare the distributions of species among migrational/dispersal groups at both these levels, as well as on a larger geographical scale. A discussion regarding the importance of these disjunctions at these geographic levels will follow.

4.3.1. Gulf of St. Lawrence Distribution

The Gulf of St. Lawrence distribution patterns of migrational/dispersal groups reflect the ecologies of the component species and these are generally similar for all the groups except 'migration from the south'.

Species having migrated from the south are primarily species of forested and lowland habitats. Since these habitats are widely distributed in the study area,

then these migrants are similarly widely distributed. Bryophytes whose major range is in the southern portion of the study area are generally species reaching their northern limits in eastern North America there, and are associated with the Eastern Deciduous Forest. In the study area, they are almost wholly restricted to the Acadian Forest or Great Lakes-St. Lawrence Forest Regions (Figure 1-4, page 15) (e.g., *Atrichum crispum*, *Aulacomnium heterostichum*, *Buxbaumia minakatae*, *Lejeunea ulicina*). Both forest regions are closely related to the Eastern Deciduous Forest (Rowe 1977). Bryophytes which are more widespread in the study area are associated mainly with the Boreal Forest region, and usually reach their northern limits in eastern North America north of the study area in central Labrador.

Species in the other migrational/dispersal groups do not, in general, have continuous or widespread distributions in the Gulf. These groups contain species mainly restricted to treeless vegetation, which is not widely distributed in the region. Most groups (excluding introduced species) show the highest diversities in western Newfoundland (particularly the Northern Peninsula) and Gaspé, with smaller concentrations in southern Labrador, the North Shore, and Cape Breton Island. Many species are found only as disjuncts between Gaspé and the Northern Peninsula of Newfoundland.

Many workers have attributed the Gulf of St. Lawrence distributions of

plants critical to the various migrational/dispersal hypotheses to their Wisconsin glacial history. This has been especially true for disjuncts used in support of the 'nunatak hypothesis'. Fernald (1925), in particular, noted the restriction of rare disjunct vascular plants to supposed unglaciated areas and used this to suggest species survival in (and limited postglacial migration from) these areas during the Last Glaciation. From my studies, many bryophytes in the refugial group were found to occur *only* in areas having been recently proposed or confirmed as ice-free in the Gulf of St. Lawrence (see Figure 1-3, page 12), e.g., *Andreaea nivalis*, *Moerckia blyttii*, *Oligotrichum hercynicum* (Figure 4-20). It is tempting to suggest that some of these, especially those extremely restricted in the Gulf, survived the last glaciation near where they are found today.

However, in other regions of the study area, there are no correlations between numbers of refugial bryophytes present and ice-free areas based on recent glaciological information (Brookes 1977; Grant 1977a; Rogerson 1981). Eastern Newfoundland and southern Labrador provide good examples. These regions have been postulated as ice-free areas, but relatively few localized, disjunct refugial bryophytes occur there (Figures 3-12, 3-13). The species in the refugial group found in eastern Newfoundland consist mainly of boreal or temperate bryophytes, many occurring widely within the study area (e.g., *Orthotrichum gymnostomum*, *Tetraphis geniculata*). The presence of these species, most of which are easily dispersed, might be attributed to rapid reinvasion of suitable habitats following disturbance.

The present-day Gulf distributions of most bryophytes in the refugial group (and most other migrational/dispersal groups related to the 'nunatak hypothesis') are likely more closely tied to ecological or climatic factors operating since the Last Glaciation than to occurrence today on unglaciated sites, but this does not negate their probable refugial status in the Gulf as a whole. Fire has been an important factor in the development of present vegetation patterns in the study area (Strang 1972; Wein and Moore 1977, 1979; Meades 1983) and its frequency would certainly have eliminated some relictual bryophyte communities. The more important habitats for refugial disjunct bryophytes are in unburned climax vegetation types such as the alpine, moss and limestone heaths described by Meades (1983). Alpine and limestone heaths are especially common in the Long Range Mountains and the coastal plain of the Northern Peninsula, and this may partly explain the presence of many of the disjunct bryophytes there (see Figures 3-10, 3-11, page 70). Such areas with high diversities of disjunct relics would have been refugia for these plants not only during the glaciation, but during the Holocene as well.

Geological factors are also important in the Gulf distributions of many disjuncts. Large areas of the North Shore and southern Labrador were inundated by the sea immediately following the disappearance of glacial ice (Dubois 1977), and this might explain the lack of critical disjuncts in those areas. The presence of some rare disjuncts (e.g., *Encalypta longicolla*, *Metacalypogeia schusterana*,

Schistidium trichodon) there today is best explained as postglacial dispersal from relictual populations elsewhere within the study area.

Studies of the substrates of the disjunct vascular plants showed these to be mainly restricted to soils of basic reaction and this was used to explain their rarity in the Gulf (see especially Wynne-Edwards 1937, Scoggan 1950, Rune 1954, Damman 1965). The disjunct bryophytes, especially those important to the refugial history do *not* show a similar pattern, and occur on soils and rocks of many different types. It is particularly significant that the species most critical to the refugial hypothesis (e.g., *Andreaea nivalis*, *Moerckia blyttii*, *Oedipodium griffithianum*) are found *only* on siliceous rocks, or soils derived from them.

Scoggan (1950), Rune (1954), Damman (1965, 1976), and others have stated that present climate and soils can adequately explain the northern and disjunct element in the Gulf of St. Lawrence flora. Ecological factors no doubt explain the present distribution of the disjunct bryophytes within the Gulf of St. Lawrence, but ecology cannot fully explain the patterns of disjunction seen at larger geographical scales, such as eastern North America. Raup (1941, p.196) has aptly stated, "It [ecology] may account for much of the local distribution of isolated species, but does not clarify their means of arriving at their present areas or the reasons for not having spread to larger areas."

4.3.2. Eastern North American Distributions

The disjunct bryophytes of the Gulf of St. Lawrence fell into 22 of the 27 possible sub-elements. This indicates the varied (and complicated) eastern North American distributions of many of the Gulf disjuncts.

A relatively high proportion (38%) of the total bryophyte species present in the Gulf of St. Lawrence show a disjunction to this region. It is particularly surprising that the largest single disjunct migrational/dispersal group is that supporting the hypothesis of survival of bryophytes in Gulf of St. Lawrence refugia, a result strongly contrasting with the evidence from vascular plants for such survival (Drury 1969, Rousseau 1974). The diversity (six sub-elements) of the eastern North American distribution types showing an isolated Gulf centre is of considerable importance. Clearly, a simplistic model of migration from the south, as suggested by Wynne-Edwards (1937), Scoggan (1950), and Rune (1954), cannot adequately explain this variation.

Migrants from the south are also important, and comprise 30% of bryophyte disjuncts in the Gulf. Although this migrational/dispersal group is comprised of eight sub-elements, the continuous distributions from regions south of the Gulf and the generally widespread distributions in those regions strongly suggests postglacial northward migration.

About 26% of the disjuncts (in five sub-elements) supported two histories

(migrants from the west and/or survival in refugia, migrants from the west and/or north, and migrants from the north in part). The proximity of the Gulf ice-free areas to the southern margin of the icesheet has contributed to the difficulties in interpreting the distribution of some plants in these groups, particularly those species having a disjunction from the Gulf to the Great Lakes. Species with this disjunction comprise the majority of bryophytes whose eastern North American distribution support either of two histories. Their eastern North American distributions show that they have had very complex migrational/dispersal histories and, it is therefore difficult to explain their presence in the Gulf with a single model of postglacial migration. Some of these species did survive south and/or west of the Gulf during glaciation, as subfossil evidence shows (Miller 1980a, 1980b), but there is no evidence to show that those populations were the source(s) for all the populations in the study area.

Some species in the migrants from the west and/or survival in refugia group may have survived in refugia and this is strongly suggested by their overall eastern North American distributions. Some have wide disjunctions to the arctic, either to the coastal mountains of northern Labrador (e.g., *Coscinodon cribrosus*, *Miehlichhoferia miehlichhoferi*, *Pseudoleskea patens*) or to the Greenlandic arctic (e.g., *Dryptodon patens* (Figure 4-36), *Orthotrichum pallens*, *Solenostoma sphaerocarpum*).

Coscinodon cribrosus (Figure 4-37) and *Miehlichhoferia miehlichhoferi* have extreme disjunctions from the Gulf to all three other eastern North American centres. These are difficult to explain by ecology. Both species have specialized ecologies (Brassard 1969; Ireland and Crum 1976), and both produce sporophytes infrequently. These factors may help explain the species restriction in Eastern North America and suggests limited postglacial dispersal from regions known to have had ice-free areas during the Last Glaciation. Other species, for example *Orthotrichum alpestre* and *Grimmia hartmanii* (Figure 4-38), also show strongly isolated populations in the Gulf. Both are boreal species (Vitikainen 1969; Lewinsky 1977) and should occur more continuously northwards to the arctic, and westwards to the Great Lakes. Their disjunction to the Gulf may be due to slow dispersal of the species to new areas despite the sometimes abundant production of spores and/or brood bodies. The southern disjunctions of other species, like *Grimmia anodon*, *Orthotrichum pallens*, and *O. rupestre*, having boreal or temperate affinities are similarly difficult to explain and one would also expect to find these in intervening areas.

As with bryophytes disjunct to the west, it is difficult to show that bryophytes with continuous distributions from the arctic (e.g, migrants from the north and/or west group, and migrants from the north in part) did in fact migrate to the Gulf from that region. Increasing geomorphological evidence points to ice-free areas (Late Wisconsin at least) along much of the Labrador coast (Ives 1978;

Figure 4-36. The North American distribution of *Dryptodon patens*
(modified from Steere (1938)).

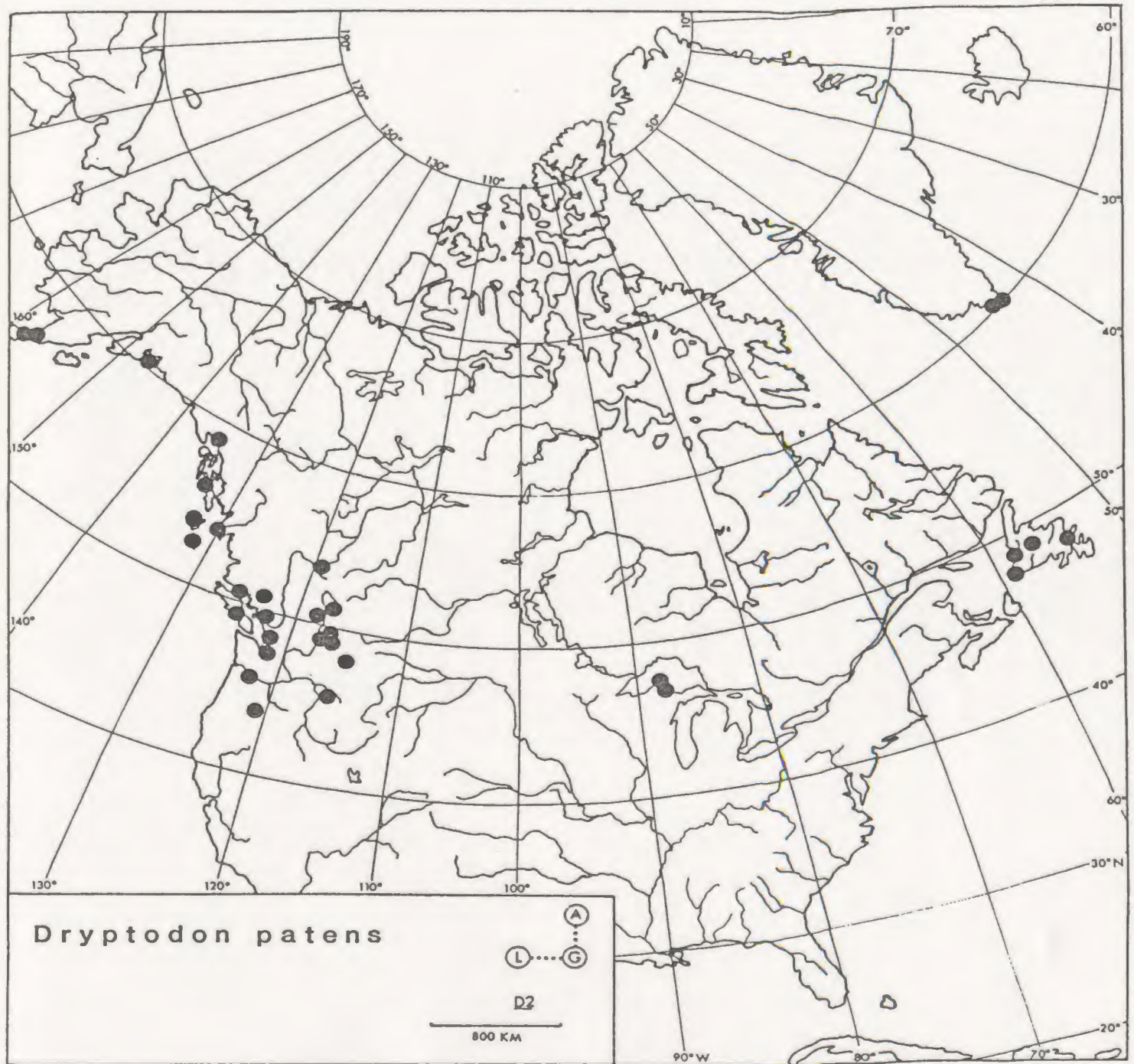
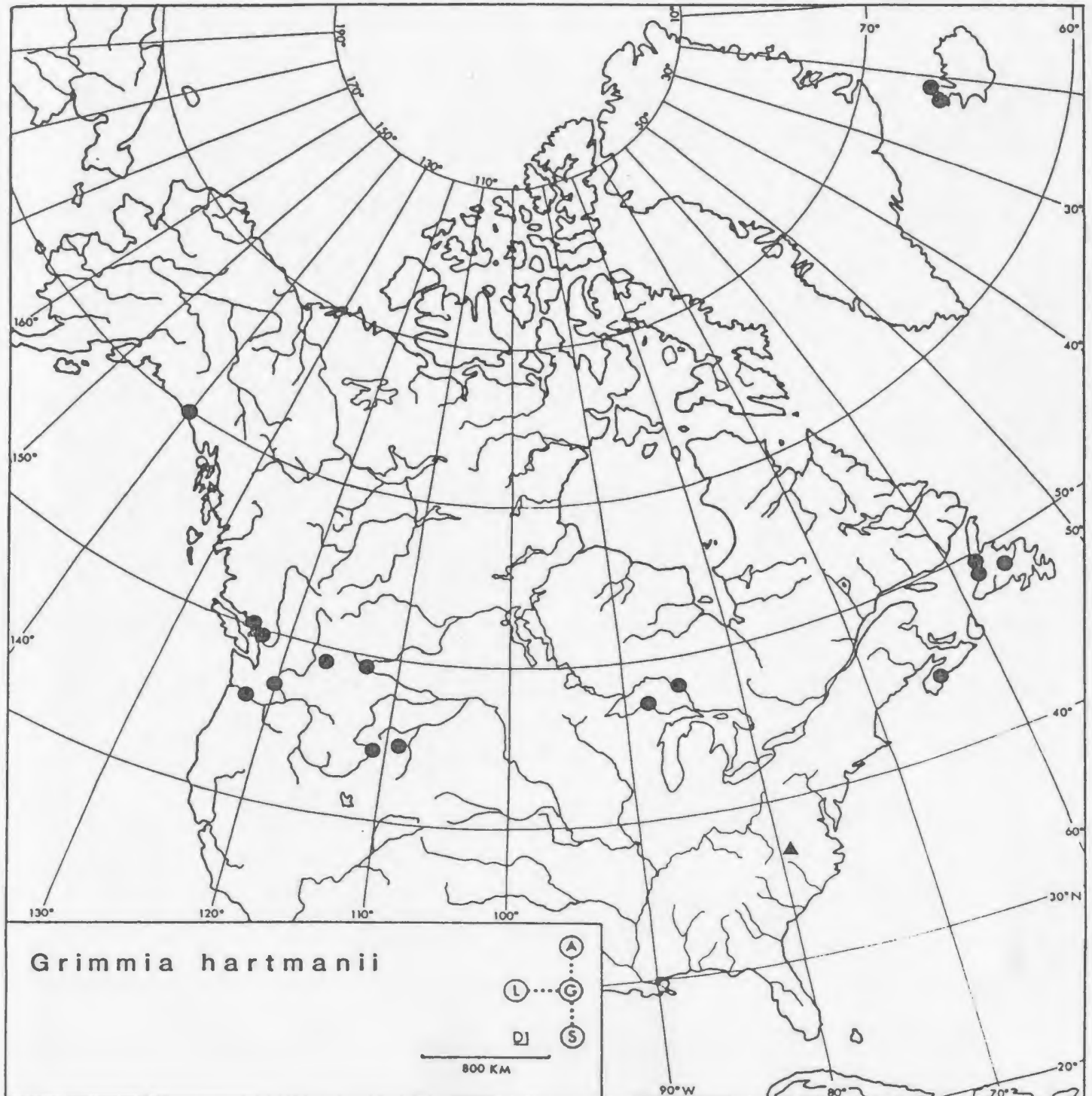


Figure 4-37. The North American distribution of *Coscinodon*
cribrosus (expanded after Ireland and Crum (1976)). The species
is also known from Arizona and the Aleutian Islands (dots not
shown).



Figure 4-38. The North American distribution of *Grimmia*

hartmanii (expanded from Vitikanen (1969); also reported from Greenland). Dots are *G. hartmanii* var. *anomala*; triangle is *G. hartmanii* var. *hartmanii*.



Rogerson 1981) and these may have provided several source areas from which populations could have recolonized adjacent glaciated land in the Gulf region. Evidence from offshore palynological records in Cartwright Saddle (off southeastern Labrador) suggests that tundra vegetation existed on nearby land at 21,000 years B.P. (Vilks and Mudie 1978) when the Last Glaciation was near its maximum extent. Thus, species with continuous distribution from the Gulf to the arctic could have survived in refugia on the coast of Labrador as well as having survived in the Gulf and their present Gulf distribution could have resulted from postglacial migration from several possible ice-free areas.

Possible survivors in refugia within the migrants from the north group would mainly include bryophytes with restricted distributions in the arctic and those characteristically associated with late snowbed species whose distributions in eastern North America strongly support survival in refugia, e.g., *Andreaea blyttii*, *Conostomum tetragonum*, *Kiaeria falcata*, *K. glacialis*, *K. starkei*, *Pleuroclada albescens*, *Pohlia drummondii*, *P. obtusifolia*, *Polytrichastrum sexangulare*.

Many bryophytes could have survived in the numerous ice-free areas existing in the study area during all or part of the Wisconsin Glaciation (Figure 1-3, page 12). Although the climate was colder than at present, (see Ruddiman and McIntyre 1981) studies of the Pleistocene history of British bryophytes (Dickson 1973) have provided good evidence that a rich bryoflora survived near

the Pleistocene icesheets in Britain. Studies on existing refugia and nunataks in Iceland and Norway (Lindroth 1970; Elven 1980) show that many plants (including several bryophyte species included in this study) are able to colonize and persist in sites very close to ice margins. In the Gulf, Anderson (1983) has provided palynological evidence for a very sparse tundra vegetation on the southern Burin Peninsula (Newfoundland) at 13,400 yrs. B.P. during the time of maximum glaciation in an area which was beyond the limit of late Wisconsin ice (Tucker and McCann 1980). Little is known of the vegetation of the region prior to this date.

Three main types of ice-free areas may have existed in the Gulf of St. Lawrence during the Wisconsin glaciations: (1) nunataks, mountain-top 'islands' surrounded by ice, (2) coastal mountain (Scandinavian type) ice-free areas (Dahl 1946), formed when high mountains border deep sea, and (3) "offshore coastal" ice-free areas (Brassard 1971), formed on continental shelves near the margins of an icesheet.

Ice-free areas of the nunatak type would have existed on the higher inland mountains of the study area such as the Shickshock Mountains of Gaspé, and the Topsail Hills of Newfoundland. Existing nunataks of this type (e.g., in Scandinavia) are generally poor in species (Elven 1980), and it is doubtful that they would have harboured an extensive flora in the Gulf of St. Lawrence during the last Glaciation.

Coastal mountain ice-free areas would have been important in those regions of the Gulf where highlands border the sea, namely, western Newfoundland, eastern Newfoundland (particularly the Burin Peninsula), Cape Breton Island, and Gaspé. Land surfaces available for colonization by plants would have existed from sea level on the forelands sheltered from the iceflow, to the summits of the coastal highlands. According to Dahl (1946), coastal ice-free areas may have had an oceanic Atlantic climate, and a rich flora of vascular plants, mosses and lichens. In the Gulf, coastal ice-free areas may have been important sites of survival for many bryophytes, particularly montane species on highlands areas.

The Grand Banks may have been a large refugium if the interpretations of Alam and Piper (1977), Grant (1977b), and Slatt (1977) are correct. These workers show that much of the Grand Banks was ice-free during the late Wisconsin. Their results have recently been challenged by the model of proposed by Quinlan and Beaumont (1981) which suggests that all of the Grand Banks was under the sea at 13,000 yrs. B.P.

If the Grand Banks was an ice-free area as the majority of glaciologists presently believe, then its southerly location and proximity to the ocean would probably have made this region considerably warmer than the coastal ice-free areas bordering the Gulf. The ice-free area in Iceland discussed by Lindroth (1970) is a present-day refugial analogue. Lindroth noted this refugium to be

diverse in species, and even able to support trees. A similar "Grand Bank" refugium would help explain the refugial group bryophyte species having primarily forest or oceanic affinities (e.g., *Antitrichia curtispindula*, *Homalothecium sericeum*, *Orthotrichum gymnostomum*, and *Tetraphis geniculata*); these are present or common in Newfoundland, but generally absent elsewhere in the Gulf. Species surviving in a Grand Banks refugium would have to be mobile, especially during deglaciation, when they would have been forced to migrate to higher land because of gradually rising sea level.

It must be emphasized that little is known of the climate of the Grand Banks during the last glaciation. CLIMAP (1981) has reconstructed the sea-surface temperatures for last glacial maximum and shown that these were cold (0-4°C for August) and equivalent to sea-surface temperatures presently found along the coasts of northern Labrador, Baffin Island and Greenland. Others, for instance Alam and Piper (1977), have shown the relatively warm Gulf Stream current impinging upon the Grand Banks during the late Wisconsin and Vilks (1981) has suggested that during the late glacial the release of glacial meltwater from the icesheets minimized the effects of the colder Labrador current on the Labrador and Scotian shelves. Presumably, this was also the case for the Grand Banks.

It is likely that a large proportion of the disjunct bryophytes in the migrants

from the south group survived glaciation as integral members of the forests existing south of the icesheets during the Last Glaciation (Delcourt and Delcourt 1981; Delcourt *et al.* 1983). Most workers believe that these existed near the icesheets during glaciation, either on the continent or on the continental shelf (Holland 1981), although it is not clear which refugium would have been most important for individual species. That large assemblages of bryophytes existed in open woodlands near the icesheet on the continent during the late-glacial has been well documented by Miller (1980a, 1980b). There is no reason to believe that similar assemblages could not have existed on the continental shelves also since Emery *et al.* (1965) reported remains of *Sphagnum* dredged from George's Bank in organic deposits dating 12,000-8,500 yr B.P.

The two most important habitats for disjunct bryophytes investigated in this study were the late snowbed and limestone barrens. The bryofloras of both habitats contain a high proportion of disjuncts, and for this reason, these habitats are discussed here in more detail.

Snowbeds were no doubt a common habitat near the icesheet margin during the Wisconsin glaciations, and bryophytes adapted to such a habitat would undoubtedly be able to persist there more readily than others. Species occurring only in snowbeds today are the most likely candidates for survival in Gulf of St. Lawrence ice-free areas during the Wisconsin glaciations. Compared to other

habitats investigated in the Gulf of St. Lawrence, late snowbeds had the largest complement of disjuncts.

Late snowbeds were investigated at three localities within the study area: on Mont Jacques-Cartier (Gaspé), on 'Big Level' in western Newfoundland, and northeast of Parsons Pond on the Long Range Mountains.

Of the 51 bryophytes found in the snowbeds of the three Gulf of St. Lawrence areas, 30 were disjuncts (as defined in this study), and these belonged to nine sub-elements (Table 4-1). The majority of the species are found in the arctic; they are either disjunctive to this region (e.g., sub-element D5) or continuous to it (e.g., sub-element C10).

Most of the disjunct bryophytes in the snowbeds had arctic or montane affinities but the montane species (19) far outnumbered the arctic species (6). More than half of the montane mosses, e.g. *Andreaea nivalis* (Figure 4-27), *Hydrogrimmia mollis*, and *Oligotrichum hercynicum*, and almost all the montane hepatics are *disjunctive* to the arctic (the Torngat Mountains or Greenland). One montane moss, *Pseudoleskea patens*, is disjunct to the Great Lakes.

Among arctic snowbed bryophytes, all except *Lophozia wenzelii* are *continuous* to the arctic; this species was also disjunct to the Great Lakes.

Table 4-1. The disjunct bryophyte sub-elements found in the Gulf of St. Lawrence snowbeds.

Sub-element	Number of species	% of total
C1	2	7
C2	1	3
C6	1	3
C7	1	3
C10	10	33
D2	3	10
D4	1	3
D5	10	33
D8	1	3
Total	30	98

In eastern North America (excluding Greenland) the following snowbed disjuncts are known from less than 10 localities: *Andreaea blyttii*, *A. nivalis*, *Hydrogrimmia mollis*, *Kiaeria falcata*, *Lophozia obtusa*, *Marsupella condensata*, *Moerckia blyttii*, *Oligotrichum hercynicum*, *Pleuroclada albescens*, *Polytrichastrum sexangulare*, *Scapania uliginosa*, and *Trematodon montanus*.

Fifteen bryophytes found in the Gulf of St. Lawrence late snowbeds are characteristic of this habitat throughout much of their world range (Polunin 1948; Gjaerevoll 1950, 1956; Arnell 1954; Nyholm 1954-1969; Mårtensson 1955, 1956; Schuster 1969, 1974; Schofield 1972, 1976; Smith 1978; Steere 1978) and all are disjuncts treated in this study: *Andreaea blyttii*, *A. nivalis*, *Anthelia juratzkana*, *Conostomum tetragonum*, *Hydrogrimmia mollis*, *Kiaeria falcata*, *Kiaeria glacialis*, *Kiaeria starkei*, *Marsupella condensata*, *Moerckia blyttii*, *Oligotrichum hercynicum*, *Pleuroclada albescens*, *Pohlia obtusifolia*, *P. drummondii*, and *Polytrichastrum sexangulare*.

In eastern North America (south of the arctic), late snowbeds are restricted to the high mountains of New England or New York, Gaspé, Newfoundland, and Labrador, and these are the only regions where one might expect such species to occur. Table 4-2 shows that Newfoundland and Gaspé have the most diverse disjunct snowbed bryofloras. Newfoundland is particularly diverse, and has nearly three times as many such species as New England, and about one and one half times as many as Labrador.

There is thus in the Gulf of St. Lawrence a community of snowbed bryophytes, all of which are disjunctive in eastern North America. Disjunct bryophyte *communities* have seldom been discussed in boreal and arctic North America. Crum (1972) described beach pool communities containing many northern and 'cordilleran' disjuncts in northern Michigan which he believed were relics from the Last Glaciation, and Steere (1965) described an assemblage of temperate disjuncts in Alaska which he thought were also glacial relics. The snowbed communities in the Gulf of St. Lawrence today are likely relics of those which existed there during the Last Glaciation.

In the Gulf of St. Lawrence region, limestone barrens are found primarily on the Northern Peninsula of western Newfoundland (FNW) with minor outliers in southern Labrador. The limestone barrens are mainly restricted to exposed coastlines where they form a narrow strip of habitat in the Gulf of St. Lawrence. The vascular flora of these barrens has long been known to botanists for its component of rare and disjunct plants (Fernald 1911). The vegetation of limestone barrens in these areas has recently been described by Meades (1983).

Limestone barrens were investigated at four localities, all on the Northern Peninsula: Port aux Choix, Bateaux Barrens, Burnt Cape, and Cape Norman. Only the data from the mosses is presented here since hepatic diversity is generally low in this habitat.

Table 4-2. Distribution of Gulf of St. Lawrence bryophytes characteristic of snowbeds in the mountainous regions of eastern North America. Nf, Newfoundland; Lb, Labrador (south of the arctic); Ga, Gaspé; Ne, New England/New York.

Species	Nf	Lb	Ga	Ne
Hepatics				
<i>Anthelia juratzkana</i>	+		+	+
<i>Marsupella condensata</i>	+		+	
<i>Moerckia blyttii</i>	+			
<i>Pleuroclada albescens</i>	+	+	+	
Mosses				
<i>Andreaea blyttii</i>	+	+	+	
<i>A. nivalis</i>	+		+	
<i>Conostomum tetragonum</i>	+	+	+	+
<i>Hydrogrimmia mollis</i>			+	
<i>K. falcata</i>	+			
<i>K. glacialis</i>	+	+	+	
<i>K. starkei</i>	+	+	+	+
<i>Oligotrichum hercynicum</i>	+			
<i>Pohlia drummondii</i>	+	+	+	+
<i>P. obtusifolia</i>	+	+	+	+
<i>Polytrichastrum sexangulare</i>	+	+		
Total	14	8	11	5

Of the 129 mosses present in the limestone barrens, 39 (30%) are disjuncts treated in this study. They belong to 11 sub-elements (Table 4-3). The majority (84%) are present in the arctic and a large proportion (22 of 33) are disjunctive to this region. Considerably smaller proportions of species are present near the Great Lakes (38%) and the southern Appalachians (13%).

The limestone barren disjunct bryoflora is characterized by species with arctic affinities, and these comprise more than half (56%) of the disjuncts occurring in the habitat. Of the 22 arctic species, 12 are disjunct from the arctic and several show extreme disjunctions from this region (e.g., *Didymodon asperifolius*, *Hypnum procerrimum*, and *Trichostomum arcticum*).

Boreal mosses are also important, though they comprise only 28% of the limestone barren disjuncts. All are present in the eastern arctic, except *Campylium halleri* and *Entodon concinnus*.

Only three disjunct montane mosses are known from the limestone barrens (*Desmatodon systilius*, *Encalypta longicolla* and *Funaria microstoma*); all show wide disjunctions from their nearest stations in the arctic.

Half (20) of the limestone barren disjuncts have been included within the refugial migrational/dispersal group, and several are known only from the limestone barrens within the Gulf of St. Lawrence: *Bryum wrightii* (Figure 4-28),

Table 4-3. The disjunct bryophyte sub-elements found in the Gulf of St. Lawrence limestone barrens.

Sub-element	Number of species	% of total

C1	1	3
C2	2	5
C5	2	5
C7	4	10
C8	2	5
C10	4	10
C14	2	5
D2	2	5
D5	16	41
D6	2	5
D8	2	5

Total	39	99

Barbula icmadophila, *Dicranum spadiceum*, *Didymodon asperifolius*, *Funaria microstoma*, *Hypnum procerrimum*, *Scorpidium turgescens*, *Splachnum vasculosum*, *Tortella arctica*, and *Trichostomum arcticum*. Several others reach their highest frequency and abundance in this habitat: *Amblyodon dealbatus*, *Drepanocladus badius*, *Hypnum bambergeri*, and *Rhytidium rugosum*.

Survival during glaciation for these species is problematical since the sites presently occupied by them were completely ice-covered during the last glacial maximum (Grant 1969, 1970), and few, similarly extensive habitats would have been present in Gulf ice-free areas during that time. However, some species could possibly have survived in unglaciated areas at higher elevations in western Newfoundland, where there are known limestone outcrops (e.g., St. John Highlands, and Killdevil Mountain at Bonne Bay). It is also possible that some species survived on travertine deposits on the unglaciated ultramafic massifs near Bonne Bay, the White Hills, or at Bay of Islands where some of the refugial mosses are known to occur (e.g., *Encalypta longicolla*, *Hypnum bambergeri*).

4.3.3. World Distributions

It is of some relevance to examine the proportions of world distributional elements within each bryophyte migrational/dispersal history, to determine relationships to distributions at the eastern North American level, and to compare them with results from vascular plant studies.

For the purposes of this study, a generalized scheme for the classification of the disjuncts into world distributional elements has been devised and is presented below. Four major elements are recognized: montane, arctic, boreal, temperate. The latter three elements contain species whose major portion of distribution fall within the arctic, boreal and temperate bioclimatic zones as defined in Walter (1973). The montane element has been defined previously (page 116). The proportion of these elements within each migrational/dispersal group for the Gulf of St. Lawrence bryophytes is summarized in Table 4-4.

The disjuncts which migrated from the south are primarily boreal and temperate in affinity, and this history has a very high proportion of species (93%) found in these two elements. Species introduced to the study area are all temperate species. Since most introductions probably came from the lowland, populated regions of Europe (Lindroth 1957), this is to be expected.

The remaining histories have high proportions of montane and arctic species (Table 4-4). Arctic species are highly represented in the migrants from the north and/or west group (Group C) while migrants from the north are comprised of about equal numbers of arctic and montane bryophytes. The refugial bryophytes (Group E), and bryophytes supporting refugia and/or migration from the west (Group D) consist of species belonging to all four world elements. The majority of bryophytes in these latter group are montane and arctic, although there is also a relatively high percentage of boreal and even some temperate species.

Table 4-4. The percentages of world elements in each migrational/dispersal history. Te, Temperate; Bo, Boreal; Mo, Montane; Ar, Arctic; Un, unknown.

Migrational/Dispersal Group	-----				
	Te	Bo	Mo	Ar	Un

A. South (80 spp.)	54	39	4	1	3
B. North (26 spp.)	-	12	38	50	-
C. North/West (16 spp.)	-	8	13	81	-
D. West/Refugia (32 spp.)	6	22	34	34	-
E. Refugia (93 spp.)	5	25	39	27	4
F. Introduced (4 spp.)	100	-	-	-	-

One might expect groups supporting in part migration from the west (groups C and D) to have similar proportions of species within the different world elements. Table 4-4 shows, however, that the world affinities of the bryophytes in these groups differ considerably. As compared to group C, group D shows much lower percentages of montane and arctic species and higher percentage of boreal species. In fact, the proportion of species in world elements in group D is more similar to those of the refugial bryophyte group species (group E) than to those of group C and would support the statement made earlier (page 159) that many species in the migrants from the west and/or survival in refugia group may have survived the last glaciation in Gulf ice-free areas.

The migrants from the north and/or west group (Group C) has the highest proportion of arctic species. All the hepatics in this migrational/dispersal group are arctic species, which agrees with the observations of Schuster (1958b) who did not recognize any montane 'cordilleran' hepatics as occurring in the Great Lakes. There are, however, two montane *mosses* in the Great Lakes area: *Grimmia torquata* and *Hygrohypnum alpestre*. *Grimmia torquata* is considered circumalpine by Schofield (1969) and *Hygrohypnum alpestre* as northern and montane by Crum and Anderson (1981).

It is significant that the groups containing the most diverse array of world elements (groups D, E) include species disjunctive from the Gulf centre to *all*

other eastern North American centres. A series of different types of variously sized ice-free areas such as would have existed in the Gulf of St. Lawrence during the Last Glaciation could be expected to have suitably diverse habitats which could provide refugia for species with different world distributional affinities. The high percentage of boreal species (e.g., *Grimmia anodon*, *Orthotrichum alpestre*, *O. pallens*) is of particular interest since boreal/temperate forest dominates the regions between the Gulf and the Great Lakes, and one would expect these species to be more continuous to that region. Floras comprising different world elements have been used to support botanical refugia on northern Ellesmere Island (Brassard 1971) and arctic Alaska (Steere 1978) and the present study yielded similar conclusions.

The similar distributions of the arctic and montane elements in eastern North America was central to the arguments against the nunatak hypothesis presented by Wynne-Edwards (1937). I have already discussed the distributional differences in the eastern North American Arctic of montane and arctic bryophyte species in some groups (page 116). Differences can also be shown in their occurrence in the Great Lakes: only 25% of the Gulf montane bryophytes occur in the Great Lakes region, as compared to 40% of the arctic species. The differences are even more pronounced when considering only those groups whose species support eastward migration of species (Groups C and D, Table 4-4). One would expect an equal proportion of arctic and montane bryophytes in these

groups if the source for these species is the Western Cordillera. Of the 48 bryophytes in these histories, 27% are montane, and almost 50% are arctic. It would seem that in the east, most montane bryophytes probably never ranged further west than the Appalachian Mountains during Glaciation. This supports the conclusion made earlier that most of the bryophytes at the Great Lakes did not migrate eastwards in a tundra corridor as envisioned by Marie-Victorin (1938), Raymond (1950), Rousseau (1953), and Whitehead (1972), and strengthens my contention that basic eastern North American distributional differences exist between arctic and montane bryophytes.

There is not much evidence for gradation of North American distributions among the arctic and montane bryophytes as Wynne-Edwards (1937) demonstrated for vascular plants. Such a gradation may exist at the eastern North American level, since members of both arctic and montane elements show varying degrees of disjunction between the Gulf of St. Lawrence and the Arctic. However, their distributions in the higher latitudes of North America are, for the most part, distinct: arctic species extend continuously across the North American arctic to Alaska, whereas montane species are absent from the central arctic.

It would appear that arctic and montane species also differ in their overall ecology. Limestone barrens are particularly important for arctic disjuncts, many of which are considered calciphilic (Tuomikoski *et al.* 1973). It is interesting that

many of Fernald's disjuncts were also arctic calciphiles (see the arguments of Wynne-Edwards, 1937). The snowbed habitat is important for montane bryophytes, which are primarily acidophilic. It is reasonable to assume that such contrasting ecological differences could not result from changes since the Last Glaciation, but rather, must have become established during the slow evolution of the species (e.g., that ecological tolerances of species evolved before the Last Glaciation).

The Gulf disjuncts have world distributions variously disjunct between four world regions: eastern Asia, western North America, eastern North America, and Europe, and most are disjunctive between all four regions, e.g., *Aulacomnium androgynum*, *Campylium halleri*, and *Oedipodium griffithianum*. A few species are disjunctive between eastern Asia and eastern North America and these have been explained as a remnant of a more widely distributed Arcto-Tertiary flora persisting in areas that have not undergone substantial geological and climatic changes for millions of years (Sharp 1971, 1972a, 1972b; Schofield 1980; Schuster 1984); there is much evidence from studies of fossil vascular plant deposits to support this idea (Matthews 1979). Other disjunct bryophytes have amphiatlantic distributions (in the wide sense, i.e., North America/Europe), and are also interpreted as being Tertiary in origin (Löve and Löve 1967). The disjunctions between all four world regions are related to the amphiatlantic and eastern North America/eastern Asia patterns, and result from extinction in portions of a

formerly more continuous range; thus most of the disjunctions at a continental scale (except arctic species, which have more or less continuous distributions in polar regions) are best explained as having developed since the Tertiary.

The majority of species which migrated to the Gulf of St. Lawrence from the south are disjunctive to western North America and this disjunction may be due mainly to Holocene climatic and vegetational changes rather than to pre-Pleistocene events. For most species, this disjunction is relatively narrow and the absence of most species in the central portion of the continent coincides with the presence of the prairie biome. Many of the species probably had wider distributions in southern and central North America within the boreal and temperate forests extending across those regions during a full glacial period (see for instance Wright 1981). The postglacial development of prairies disrupted this formerly more continuous distribution and resulted in the present-day patterns. However, most of the species are also disjunctive to other world centres. Some have amphiatlantic distributions, or are disjunct to eastern Asia, and these disjunctions are undoubtedly pre-Pleistocene in origin.

4.3.4. Synthesis and Conclusion

The importance of disjunction with respect to migrational/dispersal histories of disjunct bryophytes in the Gulf of St. Lawrence is clearly related to the geographical scale of distribution studied; as a rule, the larger the scale of the disjunctions, the farther back in time one needs to go in order to find the cause/factor responsible for the disjunction. The discussion of the distributions of the Gulf of St. Lawrence bryophyte disjuncts at different geographical scales has shown that (1) species with different eastern North American distributions (and thus different Wisconsin histories) are represented by several world elements, (2) that bryophytes which may have had different Wisconsin histories may have similar distributions at the smaller Gulf of St. Lawrence geographical scale, and, (3) that the factors giving rise to the bryophyte disjunctions at these scales are different. Presented below is a brief summary of the importance of disjunctions at different geographic scales as shown by the bryophytes used in this study:

1. *Gulf of St. Lawrence.* At this level, the disjunctions (and distributions) of bryophytes are shaped primarily by ecological factors operating in a short time span ($<10,000$ yrs.) and on a small geographic scale (few 100 km).

2. *Eastern North America.* Disjunctions at this geographic level are important for the study of migrational/dispersal histories over larger

periods of time than at the previous scale. In this study, eastern North American distributions were most important in the consideration of the histories of the disjunct bryophytes during the Wisconsin Glaciations (ca. 80,000 yrs. max.). There is much evidence for several pre-Wisconsin glacial episodes (see Ford *et al.* 1984), and these would also have contributed to species range disruptions, although it is difficult to judge to what degree present-day (and including Wisconsin) eastern North American distributions were molded by these.

3. *World*. Disjunctions at this scale are best explained by events and changes that have occurred since the Tertiary. Floristic elements thought to represent the remnants of wider distributions during this period include the Eastern Asia/Eastern North American Element, and the Circumalpine Element.

Distributions at the eastern North American scale are thus adequate and the most important for attempting to solve problems relating to Wisconsin history in the Gulf of St. Lawrence. The phytogeographic controversies of earlier workers can be attributed, at least in part, to a failure to appreciate the importance of disjunctions at different geographic levels. Workers like Wynne-Edwards (1937), Griggs (1940), Böcher (1950), Scoggan (1950), and Damman (1965) emphasized the

ecologies of the rare disjuncts at the Gulf of St. Lawrence distributional scale but used this information to explain migrational histories at the eastern North American scale, and even at the continental scale. While this explained the distribution of species in the Gulf, it failed to recognize the cause of the disjunctions at the larger geographic scales. Similarly, Marie-Victorin (1938) suggested that Cordilleran disjunctions were of Arcto-Tertiary origin, but related these to the Wisconsin history of species at the eastern North American level. Wynne-Edwards (1937) viewed the same large-scale disjunctions as a result of present-day ecological factors.

The results of my study show that the bryophyte disjuncts in the Gulf of St. Lawrence have had very different migrational/dispersal histories during the Wisconsin and postglacial times and, that while important, a single history of postglacial migration from the south during the Holocene cannot alone explain the variety of disjunctions displayed. Among the most important histories is survival of bryophytes in Gulf ice-free areas, for which this study has shown strong evidence from a large and very diverse group of species. The probable survival of a large number of bryophytes in ice-free areas of the Gulf of St. Lawrence is critical to an understanding of the present-day eastern North America distributions of many other bryophyte species that are either disjunct or continuous to this region, and most easily allows explanation of their presence there. Bryophyte migration from regions south of the Gulf is, however, almost equally important, particularly for disjunct species of temperate or boreal affinity.

Disjunct bryophytes comprise 38% of the total bryoflora of the Gulf of St. Lawrence region. The results presented in this study apply only to this group, and a study of the entire bryoflora would be needed to confirm that the migrational/dispersal histories of the disjunct bryophytes apply also to the flora as whole.

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Appendix A

Sources of data for eastern North American distributions of disjunct bryophytes occurring in the Gulf of St. Lawrence region.

This appendix summarizes, for each disjunct bryophyte, the major source(s) of data used to assign them to sub-elements, and, where necessary, gives additional unpublished distributional information for the Gulf of St. Lawrence. The following abbreviations are used for the geographical regions: AA, eastern North American Arctic; nAA, Queen Elizabeth Islands; sAA, Baffin Island; Ga, Gaspé; Gr, Greenland; GL, Great Lakes; GSL, Gulf of St. Lawrence; HB, Hudson Bay; cL, central Quebec/Labrador; sL, southern Labrador; M, Maritimes; NA, North America; eNA, eastern North America; wNA, western North America; NE, New England; Nf, Newfoundland; nQL, northern Quebec/Labrador; NY, New York; Qns, Quebec North Shore; SA, southern Appalachians. Specimens are cited only for species for which there is no published source, and these are deposited in the Bryophyte Herbarium at Memorial University (NFLD).

Musci

Aloina brevirostris (Hook. & Grev.) Kindb. Map: NA Steere (1950), Delgadillo (1975). Additional records: M, Ireland (1982).

Amblyodon dealbatus (Hedw.) B.S.G. Range: NA, Crum and Anderson (1981). Additional records: GL, Ireland and Cain (1975), Crum (1976); GSL, see Figure 4-14, page 94; NY, Ketchledge (1980).

Amphidium mougeotii (B.S.G.) Schimp. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a).

Andreaea blyttii B.S.G. Map: NA, see Figure 4-31, 138.

Andreaea nivalis Hook. Map: NA, see Figure 4-27, page 118.

Andreaea rothii Web. & Mohr. Map: NA, Schultze-Motel (1970). Additional records: cL, sL, Brassard and Weber (1978a)

Antitrichia curtispindula (Hedw.) Brid. Map: NA, Schofield (1972). Additional records: Nf, Brassard (1983a, map).

Aongstroemia longipes (Somm.) B.S.G. Map: NA, Brassard (1983a). Additional records: Gr, Nyholm (1959-1964); sL, *Belland 2460*.

Arctoa fulvella (Dicks.) B.S.G. Map: NA, Brassard (1983a). Additional records:

Ga, Belland (1984); GSL, see Figure 4-19, 101; nQL, *Hedderson 1958*.

Atrichum crispum (James) Sull. Map: NA, Schofield and Crum (1972), Schofield

(1980). Additional records: Nf, *Hedderson 609*

Aulacomnium androgynum (Hedw.) Schwaegr. Range: NA, Crum and Anderson

(1981).

Aulacomnium heterostichum (Hedw.) B.S.G. Map: NA, Schofield and Crum

(1972). Additional records: M, Ireland (1982).

Aulacomnium turgidum (Wahlenb.) Schwaegr. Map: NA, Miller (1980a).

Additional records: sL, *Belland 6217*; GSL, see Figure 4-9, page 89; Nf, *Hedderson et al. (1982)*.

Barbula icmadophila C.Müll. Range: NA, Lawton (1971). Additional records:

nAA, sAA, Kuc (1973); Nf, Tuomikoski *et al. (1973)*.

Barbula reflexa (Brid.) Brid. Range: NA, Crum and Anderson (1981).

Bartramia ithyphylla Brid. Range: NA, Crum and Anderson (1981). Additional

records: GSL, see Figure 4-11, page 91; NY, Ketchledge (1980).

Brachythecium calcareum Kindb. Range: NA, Ireland (1982). Additional

records: GL, Ireland and Cain (1975); sL, Brassard and Weber (1978a).

Brachythecium collinum (C. Muell.) B.S.G. Range: wNA, Lawton (1971).

Additional records: Ga, Belland (1984); Gr, Nyholm (1954-1969).

Brachythecium erythrorrhizon B.S.G. Range: Crum and Anderson (1981).

Additional records: GL, Ireland and Cain (1975); M, Ireland (1982); Nf, Tuomikoski *et al.* (1973); NY, Ketchledge (1980); Qns, Grondin and Melançon (1980).

Brachythecium turgidum C.J. Hartm. Range: NA, Crum and Anderson (1981).

Additional records: nAA, Brassard (1971), Ga, Comeau (1966); GL, Ireland and Cain (1975), Crum (1976); cL, Brassard and Weber (1978a); sL, Belland 4104; Nf, Tuomikoski *et al.* (1973); Qns, Grondin and Melançon (1980).

Brotherella recurvans (Mx.) Fl. Range: NA, Crum and Anderson (1981).

Bryhnia novae angliae (Sull.) Grout. Range: NA, Crum and Anderson (1981).

Additional records: sL, Brassard and Weber (1978a).

Bryum alpinum With. Range: NA, Crum and Anderson (1981). Additional

records: Nf, Tuomikoski *et al.* (1973); NE, Crum and Anderson (1981).

Bryum miniatum Lesq. Range: NA, Crum and Anderson (1981). Additional

records: GL, Ireland and Cain (1975); Nf, Tuomikoski *et al.* (1973).

Bryum muehlenbeckii B.S.G. Range: NA, Crum and Anderson (1981).

Additional records: Gr, Nyholm (1954-1969).

Bryum warneum (Rohl.) Brid. Range: NA, Shaw and Marcotte (1982).

Bryum wrightii Sull. & Lesq. Map: NA, see Figure 4-28, page 122.

Buxbaumia aphylla Hedw. Map: NA, Schofield (1974).

Buxbaumia minakatae Okam. Map: NA, Schofield and Crum (1972).

Additional records: Nf, Brassard (1975).

Calliergon sarmentosum (Wahlenb.) Kindb. Map: NA, Karcmarz (1971).

Additional records: sAA, Brassard *et al.* (1979); Ga, Lepage (1946); HB, Wynne and Steere (1943); cL, sL, nQL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973, map); NE, NY, Crum and Anderson (1981).

Calliergon trifarium (Web. & Mohr.) Kindb. Map: NA, Karcmarz (1971).

Additional records: sAA, Brassard *et al.* (1979; nAA, Brassard (1971); HB, Wynne and Steere (1943; cL, Brassard and Weber (1978a); NY, Ketchledge (1980).

Calliergon wickesiae Grout. Map: NA, see Figure 4-32, page 140.

Campylium halleri (Hedw.) Lindb. Range: NA, Crum and Anderson (1981).

Additional records: Qns, Belland 6335.

Campylium radicale (P.-Beauv.) Grout. Range: NA, Crum and Anderson (1981).

Campylopus atrovirens (Hornsch.) Mitt. Map: NA, Frahm (1980). Additional records: Nf, Belland and Brassard (1981, map).

Campylopus schimperi Milde. Map: NA, Frahm and Vitt (1978), Frahm (1980). Additional records: Nf, Tuomikoski *et al.* (1973).

Campylostelium saxicola (Web. & Mohr.) B.S.G. Range: NA, Crum and Anderson (1981). Additional records: M, Ireland (1982).

Catoscopium nigratum (Hedw.) Brid. Map: NA, Miller (1980a). Additional records: Qns, Grondin and Melançon (1980); sL, Belland 4162; Nf, Tuomikoski *et al.* (1973).

Cinclidium subrotundum Lindb. Map: NA, Mogensen (1973). Additional records: cL, sL, nQL, Brassard and Weber (1978a); Nf, Hedderson *et al.* (1982).

Cirriphyllum piliiferum (Hedw.) Grout. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a).

Conostomum tetragonum (Hedw.) Lindb. Range: NA, Crum and Anderson (1981). Additional records: nAA, Brassard (1971); HB, Wynne and Steere

(1943); cL, nQL, Ireland *et al.* (1980); cL, sL, NQL, Brassard and Weber (1978a); Nf, Brassard (1975), Belland (1983).

Coscinodon cribrosus (Hedw.) Spruce. Map: NA, Ireland and Crum (1976).

Additional records: Nf, Belland and Brassard (1981); nQL, Brassard and Weber (1978a).

Ctenidium molluscum (Hedw.) Mitt. Map: NA, Steere (1979). Additional records: Nf, Belland and Brassard (1981).

Cynodontium jenneri (Howie) Stirt. Range: wNA, Lawton (1971). Additional records: Nf, Tuomikoski *et al.* (1973).

Cynodontium strumulosum C. Muell. & Kindb. Range: wNA, Lawton (1971). Additional records: HB, Wynne and Steere (1943; Nf, Tuomikoski *et al.* (1973).

Cyrtomnium hymenophylloides (Hüb.) Kop. Range: NA, Crum and Anderson (1981). Additional records: Ga, Belland 5121; M, Ireland (1982), Belland (1984); Nf, Brassard and Weber (1977); nQL, Brassard and Weber (1978a).

Desmatodon latifolius (Hedw.) Brid. Range: NA, Crum and Anderson (1981). Additional records: Ga, Lepage (1945); sL, Belland 2507; Nf, Tuomikoski *et al.* (1973), Fife and Brassard (1980), Belland (1981).

Desmatodon laureri (Schultz) B.S.G. Range; wNA, Lawton (1971). Additional records: nAA, Steere (1947); Nf, Belland (1981).

Desmatodon leucostomus (R.Br.) Berggr. Range: NA, Steere (1947). Additional records: nAA, Brassard (1971); Nf, Hedderson *et al.* (1982); nQL, Brassard and Weber (1978a).

Desmatodon systilius Schimp. Range: NA, Crum and Anderson (1981). Additional records: nAA, sAA, Steere (1947); Nf, Tuomikoski *et al.* 1973, Fife and Brassard (1980).

Dichelyma capillaceum (With.) Myr. Range: NA, Crum and Anderson (1981). Additional records: GSL, see Figure 4-3, page 82, cL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973).

Dicranella cerviculata (Hedw.) Schimp. Range: NA, Crum and Anderson (1981). Additional records: sAA, Brassard 14503; sL, cL, nQL, Brassard and Weber (1978a).

Dicranella palustris (Dicks.) Warb. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a); Nf, Weber and Brassard (1976, map); also reported from Greenland.

Dicranella rufescens (With.) Schimp. Range: NA, Crum and Anderson (1981).

Dicranella subulata (Hedw.) Schimp. Range: NA, Crum and Anderson (1981).

Additional records: Ga, Lepage (1945); Gr, Nyholm (1954-1969); GL, Crum (1976); cL, Brassard and Weber (1978a); M, Ireland (1982); Nf, Tuomikoski *et al.* (1973).

Dicranodontium denudatum (Brid.) Williams. Range: NA, Crum and Anderson (1981). Additional records: Nf, Brassard (1983a, map).

Dicranum acutifolium (Lindb. & Arnell) Weinm. Map: NA, Peterson (1979).

Additional records: Ga, *Belland 5378*; cL, nQL, Ireland *et al.* (1980); Nf, *Belland* (1983).

Dicranum angustum Lindb. Range: NA, Tuomikoski *et al.* (1973). Additional records: Nf, Tuomikoski *et al.* (1973); sL, cL, Brassard and Weber (1978a).

Dicranum elongatum Schwaegr. Map: NA, Peterson (1979). Additional records: Qns, *Belland 6408*.

Dicranum groenlandicum Brid. Map: NA, Peterson (1979). Additional records: Qns, *Belland 6470*.

Dicranum leioneuron Kindb. Map: NA, Peterson (1979). Additional records: nQL, Ireland *et al.* (1980); sL, cL, Brassard and Weber (1978a).

Dicranum majus Sm. Map: NA, Peterson (1979). Additional records: Gr, Ireland (1982); GL, Ireland and Cain (1975); nQL, Ireland *et al.* (1980); also known from the Montreal area (Lepage 1945).

Dicranum spadiceum Zett. Range: NA, Steere (1947). Additional records: sL, cL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973).

Didymodon asperifolius (Mitt.) Crum. Map: NA, Schofield (1972).

Diphyscium foliosum (Hedw.) Mohr. Range: NA, Crum and Anderson (1981). Additional records: Ga, Favreau 8205952; Nf, Tuomikoski *et al.* (1973), Belland (1981).

Distichium inclinatum (Hedw.) B.S.G. Range: NA, Crum and Anderson (1981), Ireland (1982). Additional records: sAA, Brassard *et al.* (1979); nAA, Brassard (1971); Ga, Lepage (1945); GL, Ireland and Cain (1975); sL, cL, nQL, Brassard and Weber (1978a); Qns, Grondin and Melancon (1980).

Ditrichum lineare (Sw.) Lindb. Range: NA, Crum and Anderson (1981). Additional reports: cL, Brassard and Weber (1978a), Ireland *et al.* (1980).

Drepanocladus badius (C.J. Hartm.) Roth. Map: NA, Janssens (1981). Additional records: sL, Kucyniak (1958).

Drummondia prorepens (Hedw.) E.G. Britt. Map: NA, Schofield and Crum (1972). Additional records : Ga, Favreau 82060609; M, Ireland (1982).

Dryptodon patens (Hedw.) Brid. Map: NA, see Figure 4-36, page 161.

Encalypta longicolla Bruch. Map: NA, Brassard (1983a). Additional records: Qns, Belland 6345.

Entodon concinnus (De Not.) Par. Map: NA, Brassard (1983a). Additional records: M, Belland (1984); Nf, Belland and Brassard (1981, map).

Ephemerum serratum (Hedw.) Hampe. Map: NA, Schofield (1974). Additional records: M, Ireland (1982).

Fissidens cristatus Mitt. Range: NA, Crum and Andeson (1981). Additional records: Ga, Lepage (1945).

Funaria microstoma Šhimp. Map: NA, Fife (1979). Additional records: reported from Greenland.

Grimmia anodon B.S.G. Map: NA, Ireland and Miller (1982).

Grimmia atrata Hoppe & Hornsch. In North America, so far known only from nQL (Brassard and Weber 1978a) and Henley Harbour, sL (Belland 2566).

Grimmia donniana Sm. Range: NA, Crum and Anderson (1981). Additional records: sAA, *Brassard 14559*; Ga, *Belland 5292*; cL, nQL, Brassard and Weber (1978a); sL, *Belland 2417*; M, *Belland 6620*; Nf, *Belland 4255*.

Grimmia hartmanii Schimp. Map: NA, see Figure 4-38, page 165.

Grimmia incurva Schwaegr. Range: NA, Crum and Anderson (1981).

Additional records: Ga, *Belland 6573*; Gr, *Benninghoff and Robins 8089*; M, *Belland 6621*; Nf, *Belland 6573*; nQL, *Hedderson 1859*; NE, H. Crum, pers. comm. 1983.

Grimmia tenerrima Ren. & Card. Range: NA, Crum and Anderson (1981).

Additional records: Nf, *Fife 2186*; *Belland 4326*.

Grimmia torquata Grev. Map: NA, Schofield (1972). Additional records: HB, cL, nQL, Brassard and Weber (1978s); Nf, Brassard (1983a, map).

Grimmia unicolor Grev. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a).

Gyroweisia tenuis (Hedw.) Schimp. Range: NA, Crum and Anderson (1981).

Additional records: Nf, Belland and Brassard (1981).

Herzogiella striatella (Brid.) Iwats. Map: NA, Ireland (1969). Additional

records: Gr, Nyholm (1954-1969); Nf, Tuomikoski *et al.* (1973); Qns, Grondin and Melancon (1980).

Heterocladium dimorphum (Brid.) B.S.G. Range: NA, Crum and Anderson (1981). Additional records: Gr, Nyholm (1954- 1969); sL *Belland 2704*.

Homalia trichomanoides (Hedw.) B.S.G. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a).

Homalothecium sericeum (Hedw.) B.S.G. Range, NA, Crum and Anderson (1981). Additional records: Nf, Brassard and Weber (1977, map).

Hydrogrimmia mollis Loeske. Map: NA, Schofield (1972). Additional records: nQL, *Hedderson 2060*.

Hygrohypnum alpestre (Hedw.) Loeske. Range: NA, Crum and Anderson (1981). Additional records: sAA, Brassard *et al.* (1979); cL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973, map).

Hygrohypnum bestii (Bryhn.) Broth. Map: NA, Schofield (1980).

Hygrohypnum molle (Hedw.) Loeske. Range: NA, Crum and Anderson (1981). Additional records: Gr, Nyholm (1954-1969); cL, Brassard and Weber (1978a).

Hygrohypnum ochraceum (Wils.) Loeske. Range: NA, Crum and Anderson (1981). Additional records: sAA, Brassard *et al.* (1979); nAA, Steere (1947); cL, sL, nQl, Brassard and Weber (1978a).

Hygrohypnum smithii (Lilj.) Broth. Range: NA, Crum and Anderson (1981).

Hylocomium umbratum (Hedw.) B.S.G. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a).

Hypnum bambergeri Schimp. Map, NA, Steere (1979). Additional records: Nf, Tuomikoski *et al.* (1973, map), Belland and Brassard (1981).

Hypnum imponens Hedw. Map: NA, Schofield (1972). Additional records: cL, Brassard and Weber (1978a), Nf, Tuomikoski *et al.* (1973, map).

Hypnum procerrimum Mol. Map: NA, Schofield (1980).

Isopterygiopsis muelleriana (Schimp.) Iwats. Map: NA, Steere (1978). Additional records: cL, Brassard and Weber (1978a), Tuomikoski *et al.* (1973), Brassard and Weber (1978b).

Isopterygium distichaceum (Mitt.) Jaeg. & Sauerb. Map: NA, Ireland (1969). Additional records: GSL, see Figure 4-4, page, 82.

Isopterygium elegans (Brid.) Lindb. Map: NA, see Figure 4-26, page 112.

Isopterygium tenerum (Sw.) Mitt. Map: NA, Ireland (1969). Additional records:
M, Ireland (1969).

Isopterygium alopecuroides (Dubois) Isov. Range: NA, Allen (1982).

Isothecium stoloniferum Brid. Map: NA, Allen (1983).

Kiaeria blyttii (Schimp.) Broth. Range: NA, Crum and Anderson (1981).

Additional records: Ga, *Belland 5501*; cL, *Belland 5824*; sL, *Belland 2459*;
Nf, Belland and Brassard (1980b), Belland (1983); nQL, Brassard and Weber
(1978a).

Kiaeria falcata (Hedw.) Hag. Range: wNA, Lawton (1971). Additional records:
cL, *Belland 5789*; Nf, Belland (1983); nQL, *Hedderson 1890*.

Kiaeria glacialis (Web. & Mohr.) Hag. Range: NA, Steere (1978). Additional
records: sAA, Brassard *et al.* (1979); Ga, *Belland 5512*; Gr, Nyholm
(1954-1969); cL, nLQ, Ireland *et al.* (1980); sL, *Belland 2590*; Nf, Belland
(1984).

Kiaeria starkei (Web. & Mohr.) Hag. Range: NA, Crum and Anderson (1981).
Additional records: Gr, Nyholm (1954-1969); cL, sL, nQL, Brassard and
Weber (1978a).

Lescuraea saxicola (B.S.G.) Lor. Range: NA, Crum and Anderson (1981).

Additional records: cL, nQL, Brassard and Weber (1978a); sL, *Belland 4177*; Nf, *Belland 4269*.

Miehlichhoferia miehlichhoferi (Hook.) Loeske. Range: NA, Crum and

Anderson (1981). Additional records: Nf, Hedderson *et al.* (1982) (as *M. elongata*), *Hedderson 690*; nQL, Brassard and Weber (1978a)

Miehlichhoferia macrocarpa (Drumm.) Jaeg. & Sauerb. Map: NA, Brassard and Hedderson (1983).

Myrinia pulvinata (Wahlenb.) Schimp. Range: NA, Crum and Anderson (1981).

Myurella sibirica (C. Muell.) Reim. Range: NA, Crum and Anderson (1981).

Additional records: sL, *Belland 4206*; Qns, Grondin and Melancon (1980).

Myurella tenerrima (Brid.) Lindb. Range: AA, Brassard (1971); wNA, Lawton

(1971). Additional records: Ga, *Belland (1984)*; GL, Ireland and Bellolio-Trucco (1979); cL, nLQ, Brassard and Weber (1978a), Ireland *et al.* (1980).

Neckera pennata Hedw. Map: NA, Schofield (1974).

Oedipodium griffithianum (Dicks.) Schwaergr. Map: NA, Brassard (1983a).

Additional records: Gr, Mogensen and Lewinsky (1981).

Oligotrichum hercynicum (Hedw.) DC. Map: NA, Brassard (1983a). Additional records: GSL, see Figure 4-20, page 101; M, Allen (1984); nQL, *Hedderston 1711*.

Orthothecium chryseum (Schultes) B.S.G. Range: wNA, Lawton (1971).

Additional records: sAA, Brassard *et al.* (1979); nAA, Brassard (1971); Ga, Belland (1984); nQL, Ireland *et al.* (1980).

Orthothecium strictum Lor. Range: NA, Steere (1978). Additional records:

nAA, Brassard (1971); sAA, Brassard *et al.* (1979); GL, Ireland and Bellolio-Trucco (1979); GSL, see Figure 4-18, page 99.

Orthotrichum alpestre B.S.G. Map: NA, Brassard (1983a). Additional records:

sL, *Belland 4203*; Nf, *Hedderston 270*.

Orthotrichum gymnostomum Bruch. Range: NA, Crum and Anderson (1981).

Additional records: Brassard and Weber (1977, map).

Orthotrichum pallens Brid. Map: NA, Vitt (1970), Lewinsky (1977). Additional

records: Nf, *Brassard 13989, 133071, 13720*.

Orthotrichum stramineum Hornsch. Range: NA, Brassard (1984b). Additional

records: GSL, see Figure 4-18, page 99.

Orthorichum pylaisii Brid. Map: NA, Vitt (1970). Additional records: sL, *Belland 2525*; Nf, *Weber 2398*; nQL, Brassard and Hancock (1975).

Orthotrichum rupestre Schwaegr. Range: NA, Vitt (1974), Crum and Anderson (1981).

Orthotrichum sordidum Aust. Map: NA, Vitt (1970), Lewinsky (1977).

Philonotis yezoana Card. Map: NA, Brassard (1983a).

Physcomitrium immersum Sull. Range: NA, Crum and Anderson (1981).
Additional records: M, Ireland (1982).

Plagiobryum zierii (Hedw.) Lindb. Range: NA, Crum and Anderson (1981).
Additional records: Gr, Nyholm (1954-1969); GSL, see Figure 4-7 page 87;
nQL, Brassard and Hancock (1975).

Plagiothecium cavi-folium (Brid.) Iwats. Map: M, Ireland (1969). Additional records: reported from Greenland; cL, nQL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973).

Plagiothecium laetum B.S.G. Map: NA, Ireland (1969). Additional reports: reported from Greenland; cL, nQL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973).

Platydictya confervoides (Brid) Crum. Range: NA, Crum and Anderson (1981).

Additional records: Ga, Comeau (1966); M, Ireland (1982).

Pleuridium subulatum (Hedw.) Rabh. Range: NA, Crum and Anderson (1981).

Additional records: M, Ireland (1982).

Pohlia andalusica (Hohn.) Broth. Map: NA, Shaw (1981). Additional records:

M, Ireland (1982).

Pohlia annotina (Hedw.) Lindb. Map: NA, see Figure 4-25, page 110.

Additional records: Gr, Crum and Anderson (1981);

Pohlia drummondii (C. Muell.) Andr. Map: NA, Shaw, (1981). Additional

records: GSL, see Figure 4-8, page 87.

Pohlia elongata Hedw. Map: NA, Shaw (1982). Additional records: reported

from Greenland; sL, *Belland 2787*.

Pohlia filiiformis (Dicks.) Andr. Range: NA, Crum and Anderson (1981).

Additional records: cL, Brassard and Weber (1978a); M, Ireland (1982),

Belland (1984).

Pohlia lescuriana (Sull.) Grout. Map: NA, Shaw (1982). Additional records:

Ireland (1982).

Pohlia obtusifolia Brid. (L. Koch). Map. NA, Shaw (1982). Additional records:
Ga, Belland 5508, 5470.

Polytrichastrum sexangulare (Brid.) G.L. Smith. Range: wNA, Lawton (1971).
Additional records: sAA, Brassard *et al.* (1978); Ga, report in Belland
(1983) is incorrect; GSL, see Figure 4-6, page 84; cL, Brassard and Weber
(1978a), Ireland *et al.* (1980); Nf, Belland (1983); nQL, Brassard and Weber
(1978a).

Pottia truncata (Hedw.) Fuernr. Map: NA, Schofield (1974). Additional records:
M, Ireland (1982).

Pseudeskea patens (Lindb.) Kindb. Range: NA, Crum and Anderson (1981).
Additional records: Ga, Belland (1984); GSL, see Figure 4-15, page 96; nQL,
Brassard and Weber (1978a).

Pseudeskeella catenulata (Schrader) Kindb. Map: NA, Lewinsky (1974).
Additional records: GL, Ireland and Bellolio-Trucco (1979); sL, Brassard
and Weber (1978a); Nf, Belland and Brassard (1981).

Pseudeskeella tectorum (Brid.) Broth. Map: NA, Lewinsky (1974). Additional
records: Ga, Crum and Anderson (1981); sL, Belland 4145; Qns, Grondin
and Melançon (1980).

Pseudoscleropodium purum (Hedw.) Fleisch. Map: NA, Schofield (1980).

Additional records; Nf, Brassard (1983c).

Pylaisiella intricata (Hedw.) Grout. Range: NA, Crum and Anderson (1981).

Additional records: see Figure 4-2, page 80.

Pylaisiella selwynii (Kindb.) Crum. Range: NA, Crum and Anderson (1981).

Additional records: cL, Brassard and Weber (1978a); Nf, Tuomikoski *et al.* (1973), Belland and Brassard (1981).

Racomitrium heterostichum (Hedw.) Brid. Range: NA, Crum and Anderson

(1981). Additional records: sAA, Brassard *et al.* (1979); cL, sL, nQL, Brassard and Weber (1978a).

Racomitrium microcarpon (Hedw.) Brid. Range: NA, Crum and Anderson

(1981) (as *R. heterostichum* var. *microcarpon*). Additional records: cL, sL, Brassard and Weber (1978a).

Rhabdoweisia crispata (With.) Lindb. Map: NA, Vitt and Horton (1979).

Additional records: Ga, Belland 5388, M, Ireland (1982); Nf, Brassard and Weber (1976, map); cL, Brassard and Weber (1978a); sL, Belland 4242.

Rhizomnium punctatum (Hedw.) Kop. ssp. *chlorophyllosum* (Kindb.) Kop.

Map: NA, Koponen (1973). Additional records: Qns, Grondin and Melançon (1982).

Rhynchostegium serrulatum (Hedw.) Jaeg. & Sauerb. Range: NA, Crum and Anderson (1981). Additional records: Ga, Lepage (1946).

Rhytidiadelphus loreus (Hedw.) Warnst. Range: NA, Crum and Anderson (1981). Additional records: reported from Greenland; sL, Brassard and Weber (1978a).

Rhytidiadelphus squarrosus (Hedw.) Warnst. Range: NA, Crum and Anderson (1981). Additional records: Gr, Nyholm (1954-1969); cL, Brassard and Weber (1978a).

Rhytidium rugosum (Hedw.) Kindb. Range: NA, Crum and Anderson (1981). Additional records: cL, sL, nQL, Brassard and Weber (1978a); Nf, Belland and Brassard (1980b, map).

Schistidium maritimum (Turn.) B.S.G. Map: NA, Bremer (1980a). Additional records: cL, Brassard and Weber (1978a); eNA, Crum and Anderson (1981).

Schistidium trichodon (Brid.) Poelt. Map: NA, Bremer (1980b). Additional records: Ga, Belland (1984); Nf, Hedderson *et al.* (1982); Qns, Belland 6291.

Schistostega pennata (Hedw.) Web. & Mohr. Map: NA, Lye (1972). Additional records: M, Ireland (1982); Nf, Fife and Brassard (1980).

Scorpidium turgescens (T.Jens.) Loeske. Map: NA, Miller (1980b).

Seligeria brevifolia (Lindb.) Lindb. Map: NA, Vitt (1976). Additional records:
Nf, Norris 4590.

Seligeria calcarea (Hedw.) B.S.G. Map: NA, Vitt (1976), Vitt and Horton (1979).
Additional records: Nf, Belland 6386.

Seligeria campylopoda Macoun & Kindb. Map: NA, Vitt (1976). Additional
records; sL, Belland 4080.

Seligeria diversifolia Lindb. Map: NA, Vitt (1976). Additional records: M,
Belland (1984).

Seligeria donniana (Sm.) C. Muell. Map: NA, Vitt (1976). Additional records:
Ga, M, Belland (1984); sL, Belland 4985; Nf, Belland (1981, map); Qns,
Belland 6385.

Seligeria recurvata (Hedw.) B.S.G. Map: NA, Vitt (1976). Additional records:
M, Belland (1984), sL, Belland 4247.

Seligeria tristichoides Kindb. Map: NA, Vitt (1976). Additional records: GSL,
see Figure 4-22; page 104; M, Belland (1984); Nf, Fife and Brassard (1980).

Sphagnum angermanicum Mel. Map: eNA, Holcombe (1979).

Sphagnum pylaesii Brid. Map: NA, Schofield and Crum (1972); eNA, Maass (1966). Additional records: Gr, Crum and Anderson (1981); cL, Brassard and Weber (1978a).

Sphagnum quinquefarium (Braithw.) Warnst. Map: NA, Andrus (1979). Additional records: nQL, Brassard and Weber (1978a).

Splachnum sphaericum Hedw. Range: NA, Crum and Anderson (1981). Additional records: cl, Brassard and Weber (1978a).

Splachnum vasculosum Hedw. Range: NA, Lawton (1971). Additional records: sL, Belland 2480; Nf, Tuomikoski *et al.* (1973); nQL, Brassard and Weber (1978a).

Stegonia latifolia (Schultes) Vent. Map: NA, see Figure 4-29, page 124.

Stokesiella praelonga (Hedw.) Robins. Range: NA, Crum and Anderson (1981). Additional records: M, Ireland (1982).

Tayloria lingulata (Dicks.) Lindb. Range: NA, Crum and Anderson (1981). Additional records: cL, Brassard and Weber (1978a); Nf, Fife and Brassard (1980).

Tayloria serrata (Hedw.) B.S.G. Range: NA, Crum and Anderson (1981).

Additional records: Ga, Lepage (1946); sL, Brassard and Weber (1978a); Nf, Brassard (1975).

Tayloria splachnoides (Schwaegr.) Hook. Range: NA, Crum and Anderson (1981). Additional records: Gr, Steere (1975).

Tetraphis geniculata Milde. Map: NA, Forman (1962). Additional records: sL, Belland 4227; GSL, see Figure 4-21, page 104; Qns, Grondin and Melancon (1980).

Tetraplodon pallidus (R.Br.) Hag. map: NA, Steere (1978). Additional records: Nf, Fife and Brassard (1980), *Ahti 9590, Murray 1673*.

Tetrodontium brownianum (Dicks.) Schwaegr. Map: NA, Forman (1962), Schofield (1972). Additional records: Nf, Tuomikoski *et al.* (1973), Brassard (1975).

Thuidium tamariscinum (Hedw.) B.S.G. Range: NA, Tuomikoski *et al.* (1973), Brassard *et al.* (1976).

Timmia austriaca Hedw. Map: NA, see Figure 4-35, page 148. Additional records: GSL, see Figure 4-12, page 91.

Timmia norvegica Zett. Map: NA, Brassard (1979). Additional records: Ga, Belland 5143, M, Belland (1984).

Tortella arctica (Arn.) Crundw. & Nyh. Map: AA, Kuc (1973). Additional records: sL, NQL, Brassard and Weber (1978a); Nf, Hedderson *et al.* (1982).

Tortula muralis Hedw. Range: NA, Crum and Anderson (1981). Additional records: Nf, Brassard and Weber 1977).

Tortula norvegica (Web.) Lindb. Range: NA, Crum and Anderson (1981). Additional records: cl, sL, nQL, Brassard and Weber (1978a); Nf, Brassard and Weber (1977).

Trematodon ambiguus (Hedw.) Hornsch. Range: NA, Crum and Anderson (1981). Additional records: Gr, *Steere 62-1221*; cL, Brassard and Weber (1978a).

Trematodon montanus Belland & Brassard. Map: NA, see Figure 4-30, page 132.

Trichodon cylindricus (Hedw.) Schimp. Map: NA, Ireland (1978). Additional records: reported from Greenland; GSL, see Figure 4-16, page 96.

Trichostomum arcticum Kaal. Map: NA, Schofield (1972), as *T. cuspidatissimum* Card. & Ther. Additional records: Nf, *Hedderson 2104*.

Trichostomum crispulum Bruch. Range: wNA, Redfearn (1976). Additional records: Ga, *Belland 5059*; M, *Zander and Eckel, 10 May 1982*; Nf, Belland and Brassard (1981), *Belland 4428*.

Trichostomum tenuirostre (Hook. & Tayl.) Lindb. Range: NA, Crum and Anderson (1981). Additional records: Nf, Tuomikoski *et al.* (1973).

Ulotia coarctata (P.-Beauv.) Hamm. Map: NA, Vitt (1970).

Ulotia drummondii (Grev.) Brid. Map: NA, Vitt (1970).

Ulotia hutchinsiae (Sm.) Hamm. Map: NA, Vitt (1970). Additional records: reported from Greenland.

Ulotia phyllantha Brid. Map: NA, Vitt (1970). Additional records: Nf, Brassard (1983a, map)

Zygodon conoideus (Dicks.) Hook. & Tayl. Map: Vitt (1970). Additional records: GSL, see Figure 4-24, page 106.

Zygodon viridissimus (Dicks.) Brid. Map: NA, Vitt (1970). Additional records: Ga, Belland 6818; M, Ireland (1982); NF, Tuomikoski *et al.* (1973), Belland and Brassard (1981), Brassard 13600; Qns, Belland 6364.

Hepaticae

Anastrophyllum saxicola (Schrad.) Schust. Map: NA, Schuster (1958a, 1984). Additional records: cL, Brassard and Williams (1975).

Anthelia julacea (L.) Dumort. Map: NA, Schuster (1984).

Anthelia juratzkana (Limpr.) Trev. Map: NA, Schuster (1958a). Additional records: cL, Kallio (1969); Nf, Belland (1983); eNA, Schuster (1974); nQL, Ireland *et al.* (1980).

Barbilophozia hatcheri Loeske. Map: NA, Schuster (1958a).

Barbilophozia lycopodioides Loeske. Range: NA, Schuster (1969). Additional records: cL, nQL, Ireland *et al.* (1980).

Bazzania trilobata (L.) S.F. Gray. Range: NA, Schuster (1969). Additional records: GSL, see Figure 4-1, page 80.

Cephalozia affinis Steph. Range: NA, Schuster (1974).

Cephalozia leucantha Spr. Range: NA, Schuster (1974).

Cephalozia loitlesbergeri Schiffn. Range: NA, Schuster (1974).

Chandonanthus setiformis (Ehrh.) Mitt. Range: NA, Schuster (1969).

Additional records: GSL, see Figure 4-10, page 89; cL, nQL, Brassard and Williams (1975), Ireland *et al.* (1980).

Cladopodiella fluitans (Nees) Joerg. Range: NA, Schuster (1974).

Cladopodiella francisci (Hook.) Buch. Range: NA, Schuster (1974).

Clevea hyalina (Sommerf.) Lindb. Map: NA, Schuster (1958a).

Diplophyllum albicans (L.) Dumort. Range: NA, Schuster (1974).

Diplophyllum taxifolium (Wahl.) Dumort. Range: NA, Schuster (1974).

Additional records: nQL, Brassard and Williams (1975).

Frullania bolanderi Aust. Map: NA, Schuster (1958a, 1984). Additional records:
cL, Brassard and Williams (1975).

Gymnomitrium concinnum (Lightf.) Corda. Range: NA, Schuster (1974).

Additional records: Nf, Belland (1983); nQL, Brassard and Williams (1975).

Gymnomitrium corallioides Nees. Range. NA, Schuster (1974). Additional
records: cL, Brassard and Williams (1975); Nf, Belland 1295.

Harpanthus flotovianus (Nees) Nees. Range: NA, Schuster (1980).

Herberta adunca (Dicks.) S.F. Gray. Map: NA: Brassard and Hooper (1981).

Hygrobiella laxifolia (Hook.) Spr. Range: NA, Schuster (1974).

Lejeunea caviifolia (Ehrh.) Lindb. Range: NA, Schuster (1980).

Lejeunea ulicina (Tayl.) Gott. Range: NA, Schuster (1980).

Lophozia attenuata (Mart.) Dumort. Range: NA, Schuster (1969). Additional records: cL, Brassard and Williams (1975).

Lophozia bantriensis (Hook.) Steph. Range: NA, Schuster (1969).

Lophozia binsteadii (Kaal.) Evans. Range: NA, Schuster (1969).

Lophozia capitata (Hook.) Boulay. Range: NA, Schuster (1969).

Lophozia collaris (Nees) Schust. Range: NA, Schuster (1969).

Lophozia floerkei (Web. & Mohr.) Schiffn. Range: NA, Schuster (1969).

Lophozia heterocolpa (Thed.) Howe. Range: NA, Schuster (1969). Additional records: GSL, see Figure 4-13, page 94.

Lophozia obtusa (Lindb.) Evans. Range: NA, Schuster (1969).

Lophozia porphyroleuca (Nees) Schiffn. Range: NA, Schuster (1969). Additional records: cL, Brassard and Williams (1975).

Lophozia quadriloba (Lindb.) Evans. Map: NA, Schuster (1958a). Additional records: cL, Brassard and Williams (1975).

Lophozia wenzelii (Nees) Steph. Map: NA, Schuster (1958a). Additional records: cL, Brassard and Williams (1975).

Marsupella condensata (Hartm.) Kaal. Range: NA, Schuster (1974). Additional records: Ga, *Belland 5612*; cL, *Belland 5854*; Nf, *Belland 7049*.

Marsupella sparsifolia (Lindb.) Dumort. Map: NA, Schuster (1958a). Additional records: Nf, Belland (1983).

Marsupella ustulata (Hüb.) Spr. Range: NA, Schuster (1974). Additional records: Nf, *Belland 5642*.

Metacalypogeia schusterana Hatt. & Mizut. Map: NA, Schuster (1984). Additional records: Qns, *Belland 6336*

Moerckia blyttii (Morch) Brockm. Range: wNA, Vitt (1973). Additional records: Gr, Schuster and Damsholt (1974); GSL, see Figure 4-17, page 99.

Mylia taylori (Hook.) S.F. Gray. Map: NA, Schuster (1984). Additional records: cL, Brassard and Williams (1975).

Nardia geoscyphus (De Not.) Lindb. in Carr. Range: NA, Schuster (1969).

Nardia scalaris (Schrad.) S.F. Gray. Range: NA, Schuster (1969). Additional records: Nf, Belland (1983).

Nowellia curvifolia (Dicks.) Mitt. Map: NA, Schuster (1984). Additional records: cL, Brassard and Williams (1975).

Odontoschisma elongatum (Lindb.) Evans. Map: NA, Schuster (1958a).

Odontoschisma macounii (Aust.) Underw. Map: NA, Schuster (1958a). Additional records: Ga, Schuster (1974).

Pleuroclada albescens (Hook.) Spr. Map: Additional records: GSL, see Figure 4-5, page 84; cL, *Belland 5863*; nQL, Brassard and Williams (1975).

Sauteria alpina (Nees) Nees. Range: NA, Steere and Inoue (1978). Additional records: sAA, Steere (1947); Ga, *Schuster 10715*; Gr, Schuster and Damscholt (1974).

Scapania apiculata Spr. Map: NA, Schuster (1958a). Additional records: Ga, Schuster (1974).

Scapania crassiretis Bryhn. Range: NA, Schuster (1974). Additional records: Ga, *Belland 5457*.

Scapania cuspiduligera (Nees) Muell. Map: NA, Schuster (1958a).

Scapania gymnostomophila Kaal. Map: NA, Schuster (1958a).

Scapania hyperborea Joerg. Map: NA, Schuster (1958b). Additional records: Nf, Belland 6856.

Scapania massalongoi K. Müll. Range: NA, Schuster (1974).

Scapania paludicola Loeske & K. Müll. Range: NA, Schuster (1974). Additional records: cL, Brassard and Williams (1975).

Scapania paludosa (K. Müll) K. Müll. Range: NA, Schuster (1974). Additional records: cL, Ireland *et al.* (1980); Nf, Belland (1983).

Scapania scandica (Arn. & Buch) Macvicar. Map: NA, Schuster (1958a). Additional records: Nf, Buch and Tuomikoski (1955).

Scapania subalpina (Nees) Dumort. Range: NA, Schuster (1974).

Scapania uliginosa (Sw.) Dumort. Range: NA, Schuster (1974). Additional records: Ga, Belland 6722; Nf, Belland 6561,

Scapania umbrosa (Schrud.) Dumort. Map: NA, Schuster (1958a). Additional records: GSL, Schuster (1969).

Scapania undulata (L.) Dumort. Range: NA, Schuster (1974). Additional records: Nf, Belland (1983); nQL, Brassard and Williams (1975).

Solenostoma cordifolium (Hook.) Steph. Range: NA, Schuster (1969).

Solenostoma obovatum (Nees) Schust. Range: NA, Schuster (1969). Additional records: cL, Brassard and Williams (1975).

Solenostoma sphaerocarpum (Hook.) Steph. Map: NA, Schuster (1958a). Additional records: Ga, Schuster (1979).

Solenostoma subellipticum (Lindb.) Schust. Range: NA, Schuster (1974).

Solenomstoma triste (Nees) K. Mull. Range: NA, Schuster (1974).

Tritomaria excecta (Schmid.) Schiffn. Range: NA, Schuster (1974).

Tritomaria polita (Nees) Schiffn. Range: NA, Schuster (1974). Additional records: cL, Brassard and Williams (1975).

Tritomaria scitula (Tayl.) Joerg. Range: NA, Schuster (1974).

Appendix B

The disjunct bryophyte sub-elements in the Gulf of St. Lawrence region.

This appendix summarizes, by sub-element, the Gulf of St. Lawrence distributional information for all the disjunct species treated in this study.

The Gulf of St. Lawrence regions are listed at the top of each page, as follows: ANT, Anticosti Island; FE, eastern Newfoundland; FNE, northeastern Newfoundland; FNW, northwestern Newfoundland; FS, Newfoundland south coast; FSW, southwest Newfoundland; GAS, Gaspé Peninsula; MDI, Magdalen Islands; NBC, central New Brunswick; NBN; northern New Brunswick; NBS, southern New Brunswick; NOE, southern Labrador; NOW, Quebec North Shore; NSC, central Nova Scotia; NSN, northern Nova Scotia; NSS, southern Nova Scotia; PEI, Prince Edward Island. A "+" indicates the presence of that species in a region.

The total number of disjuncts present in a region is given the bottom of the page, as well as the total number of species in the sub-element.

The Distribution of Sub-element C1 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C1 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C2 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C2 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C3 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C4 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C4 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C5 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C5 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C6 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C6 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C7 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C7 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C8 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C8 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C9 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element Cl0 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C10 Hepatics in the Gulf of St. Lawrence

[illegible]

The Distribution of Sub-element C11 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C11 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C12 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C12 Hepatics in the Gulf of St. Lawrence

[illegible]

The Distribution of Sub-element C13 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element C14 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D1 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D1 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D2 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D2 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D3 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D4 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D4 Hepatics in the Gulf of St. Lawrence

[illegible]

The Distribution of Sub-element D5 Mosses in the Gulf
of St. Lawrence

SPECIES	NBN	NBC	NBS	NSN	NSC	NSS	PEI	MDI	CAS	ANT	NOW	NOE	FE	FNE	FS	FNW	FSW
Andreaea nivalis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Antitrichia curtipendula	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Aongstroemia longipes	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0
Arctoa fulvella	0	1	0	0	0	0	0	0	1	0	0	1	1	0	0	1	1
Barbula icmadophila	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Brachythecium collinum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Bryum wrightii	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Campylopus schimperi	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	0
Cinclidium subrotundum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Cynodontium strumulosum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Cyrtomnium hymenophyllioides	1	0	0	1	1	0	0	0	1	0	0	0	0	0	0	1	1
Desmatodon laureri	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Desmatodon leucostomus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Desmatodon systilius	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Dicranum spadicum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Didymodon asperifolius	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Encalypta longicollis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1
Funaria microstoma	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Grimmia atrata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Grimmia incurva	0	1	0	0	0	0	0	0	1	0	0	0	0	0	1	1	1
Hydrogrimmia mollis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Hygrohypnum smithii	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	1
Hypnum bambergeri	0	0	0	0	0	0	0	0	1	1	1	1	0	0	0	1	1
Hypnum procerrimum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Mielichhoferia macrocarpa	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Oedipodium griffithianum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
Oligotrichum hercynicum	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	1
Orthothecium chryseum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Orthothecium strictum	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	1	1
Orthotrichum pylaisii	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	1	0
Rhytidiadelphus loreus	0	0	0	1	1	1	0	1	0	0	0	0	1	1	1	1	1
Seligeria diversifolia	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Splachnum sphaericum	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Splachnum vasculosum	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0
Stegonia latifolia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Tayloria lingulata	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Tayloria serrata	0	0	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1
Tayloria splachnoides	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
Tetraplodon pallidus	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0
Timmia norvegica	0	0	0	1	0	0	0	0	1	0	0	1	0	0	0	1	0
Tortella arctica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Trichostomum arcticum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Number of species/region:	02	02	01	06	03	02	00	01	19	01	03	09	06	04	02	13	12
Total species in this sub-element:			42														

The Distribution of Sub-element D5 Hematics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D6 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D6 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D7 Mosses in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D7 Hepatics in the Gulf
of St. Lawrence

[illegible]

The Distribution of Sub-element D8 Mosses in the Gulf
of St. Lawrence

SPECIES	NBN	NBC	NBS	NSN	NSC	NSS	PEI	MDI	GAS	ANT	NOW	NOE	FE	FNE	FS	FNW	FSW
Bryum warneum	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Cynodontium jenneri	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Dicranum leioneuron	0	0	0	1	1	0	1	0	0	0	0	1	1	1	1	1	1
Homalothecium sericeum	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0
Myrinia pulvinata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Orthotrichum gymnostomum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
Orthotrichum stramineum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Pseudoscleropodium purum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Schistidium trichodon	0	0	0	0	0	0	0	0	1	0	1	0	0	0	0	1	1
Seligeria brevifolia	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Seligeria tristichoides	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1	1
Tetraphis geniculata	0	0	1	1	1	1	1	0	1	0	1	1	1	1	1	1	1
Thuidium tamariscinum	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Trematodon montanus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Trichostomum crispulum	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1	1
Ulota drummondii	0	0	0	0	0	0	0	0	1	1	0	0	1	0	1	1	1
Ulota phyllantha	1	0	1	1	0	1	0	1	1	1	0	0	1	1	1	1	1
Zygodon conoideus	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1
Number of species/region:	03	00	02	05	03	03	02	01	06	03	03	02	10	05	04	10	10
Total species in this sub-element:	18																

The Distribution of Sub-element D8 Hepatics in the Gulf
of St. Lawrence

SPECIES	NBN	NBC	NBS	NSN	NSC	NSS	PEI	MDI	GAS	ANT	NOW	NOE	FE	FNE	FS	FNW	FSW
Scapania massalongi	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Solenostoma triste	0	0	0	1	0	0	0	0	0	0	1	0	0	0	0	0	0
Number of species/region:	00	00	00	01	01	00	00	00	00	00	01	00	00	00	00	00	01
Total species in this sub-element:	2																

Appendix C

Results of X^2 test for long range dispersal hypothesis.

The observed and expected values used in X^2 to test the hypothesis of long distance dispersal of some disjuncts to the Gulf are summarized in Tables C-1 and C-2.

Table C-1: Observed and expected frequencies used in X^2 for long distance dispersal (mosses).

Distribution Type	Dispersal Potential		
	High (<25 um)	Low (>25 um)	Total
Disjunct	82 (77.2)	7 (11.8)	89 (89.0)
Non- disjunct	368 (372.8)	62 (57.2)	430 (430.0)
Total	450 (450.0)	69 (69.0)	519 (519.0)

The disjunct hepatics showed no significant differences ($X^2 = 0.09$, $p < 0.05$) to non-disjunct species in their adaptation for long distance dispersal and a similar result was obtained for the mosses ($X^2 = 2.75$, $p < 0.05$).

Table C-2: Observed and expected frequencies used in X^2 for long distance dispersal (hepatics).

Distribution Type	Dispersal Potential		
	High (<25 um)	Low (>25 um)	Total
Disjunct	33 (32.3)	7 (7.7)	40 (40.0)
Non- disjunct	102 (102.7)	25 (24.3)	127 (127.0)
Total	135 (135.0)	32 (32.0)	167 (167.0)

